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THE NATURE OF ORGANIZING ACTION[1]

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I have reached a stage when my chief interest is in synthesis, although this is far from excluding an interest in analysis. Nature includes both; she is continually parting and recombining. Synthesis, however, has a special significance for the biologist. He remembers Claude Bernard's phrase, "life is creation"; the science of life is the science of synthesis. All nature is process, eventuating in organization: at least such a statement defines one aspect of many-sided nature. Another aspect is permanency. The two aspects are complementary; neither can exist without the other; both are necessary to organization of any kind. Part of the organization of nature carries with it the special property which we call "living." Underlying and supporting the vital type of organization are other types, extending by a regress which shows no limit to the electron and beyond.

My topic has reference to the process by which the living—as distinguished from the non-living—type of organization comes into existence. In this epoch of great scientific activity the organized living being, especially in its adult or finished state, is being resolved into its constant (or scientifically definable) components, both static and active, by a bewildering variety of analytical methods and techniques. We discover vast complexity of compo-

[1] Address of the vice-president and chairman of the Section on Zoological Sciences, American Association for the Advancement of Science, Indianapolis, December 29, 1937.

sition and activity, subject to an order and constancy which never fail to arouse our wonder. Analysis shows order to be a character of the changing or active side of nature equally with its fixed or permanent side, and no order is more impressive than that pervading the ontogenesis by which the animal or plant is progressively synthesized from apparently simple beginnings. How has this miracle of synthesis been achieved, and what does its achievement imply?

As Whewell said, to define a problem clearly is no inconsiderable step toward its solution. Consider any organic individual of higher type, such as a man, remembering that "man is a sample of nature, and just as good a sample as a solar system or an atom."[2] Each individual is a temporary construction, complexly organized according to a constant pattern, and built up from elements originally distributed at random in the environment. Primarily and fundamentally the living organism is an integrating center. Materials and energies which previously were isolated and independent come into closer association, under some kind of directive influence or compulsion, to form a characteristically organized unity. For a time this unity, no matter how complexly constituted, has a stability which is automatically conserved and a correspondingly unified complex activity. After a period of maintained organization and activity the system disintegrates—loses its wholeness or integration—and is again resolved into randomness and relative simplicity. Such a general description would apply to any higher organic individual; a cycle of integration is succeeded by one of disintegration. It may be objected that the lapsing into randomness at the end of a life cycle is an incidental rather than a necessary feature of the life process; we regard the protozoa and the germ cells as "immortal." Yet it seems generally true that organization of the highest complexity carries with it certain

[2] F. J. E. Woodbridge, "Nature and Mind," p. 237. New York: Columbia University Press, 1937.

factors or conditions which in the long run render maintenance difficult and eventually impossible. Sooner or later the integrative activity of the system declines, the second law of thermodynamics resumes its dominance and the components suffer dispersion. On the whole the contrast between randomness and integration seems to correspond, in a broad way, to the essential difference between the non-living and the living. The vital impulse—whatever its ultimate nature may be—has as its natural tendency or effect the synthesis of beings or systems which combine with complex organization and activity a persistent and characteristic unity. No such integration is discernible in the materials before they are thus assembled and unified, although certain broad elements of order are present, in correspondence with the prevalence of order in nature as a whole.

What scientific account can we give of the conditions determining this transition from randomness and incoherence to order and integration? Is it possible to single out and characterize in the clear unambiguous terms of science the factors making for this centralization and unification of elements originally dispersed without settled order in an environment?

My approach to this problem will be naturalistic, at least in its departure. We usually regard the naturalistic view as corresponding to the physical view. The physicist (as pure or uncontaminated) is an extrovert; he sees nature as a public spectacle or performance, an externality, resolvable into materials, systems and activities distributed throughout an indefinitely extended space and time. Viewed comprehensively the natural world appears as a continuum; what impresses us chiefly is its unity; it is a single being, a cosmos; its diversity is detail set in a background which is continuous and largely homogeneous. Everywhere there is apparent a certain unchanging neutral or static property, furnishing uniform conditions for motion, radiation, electrical manifestations, gravitation and the other fundamental types of physical action.

No physical entity is isolated; everything is part of a system; if there were complete isolation for any entity we could never be aware of its existence, since then it could not be a source of radiation or other action affecting the sense organs of an animal. But such a comprehensive view neglects detail; in its more usual aspect nature is a manifold, a mosaic, a complex tissue of separate systems and events. Multiplicity and diversification, rather than unity, are what chiefly impress the human observer or (I feel sure) the animal struggling for existence.

The physical view is derived primarily from external observation, but an observation which is systematized and rationalized as completely as possible. It is an idealized, simplified view, hence abstract and highly schematic; it is not nature itself (although in one sense a product of nature); it is a picture, diagram or design, standing over against nature as its model or representative, constructed, often most artfully, in a form adapted to human comprehension. As thus conceived, nature appears as a composite of elements, factors and conditions which, singly considered, have the special character of invariance, constancy or stability. This character implies unambiguity, clear-cut definability, amenability to mathematical treatment. The number of these components is usually made as small as possible (rule of parsimony). They are combined in an infinite variety of ways. What is remarkable is that far-reaching analysis, starting from widely different observational beginnings, always brings us to elements and relations which have as their most evident characters constancy and simplicity. The general conceptions agreed upon as valid by physicists (of this generation) are reached by logical processes on a basis of tested observation, and the same is true of biological conceptions. The regularities formulated by science are actually found in nature; they recur continually, hence are subject to operational test; once found and identified they are given a graphic or quantitative expression; and by extrapolations of one kind or another they lead to general conclusions having a convincing appearance of finality.

Extrapolation need be carried only a step further to lead to conclusions of the kind called metaphysical—not open to direct observational or experimental test. Whether we "believe" these or not depends on our confidence in extrapolation as a means of reaching reliable conclusions. Extrapolation assumes uniformity of conditions, continuing beyond the immediate observation. Are we justified in assuming that the uniformity which we have found experimentally through a wide range of observation extends from the observable region into the unobservable? Can we form trustworthy conclusions having reference to the unexperienced—perhaps unexperienceable—substratum or background of nature? Or are all such conclusions fallacious? It is difficult to say. With advance in methods of observation, many natural conditions whose existence has been inferred on theoretical grounds have passed from the unobservable into the observable class. For example, x-ray diffraction now gives us optical evidence of molecular constitution for many complex compounds; in a certain sense we can *see* molecular structure. In this case, the earlier extrapolations have received confirmation from observation. Atomic theory is a further case in point. Would it be safe to extend this subdividing procedure and to say that every spatial object, no matter how small, has an interior, and that its "properties" (*i.e.,* the special way in which it affects the outside world) depend on that interior? This is the method which we may call subdivisional analysis—equivalent, in the formal sense, to Whitehead's method of extensive abstraction. It would refer the constant properties of elementary objects to their special internal features of constitution. This principle would apply to the properties of stable biological entities, such as genes. There are many indications that in the chemical sense genes consist chiefly of large protein molecules; their specific properties would then be correlated with a specific molecular structure; but underlying this structure are atomic and subatomic structures each with its own

specific properties and activities. The difficulty of indefinite spatial regress then arises; and this difficulty is hardly evaded by any hypothesis of indivisible quanta, since these, being spatial or extended, ought also to have an interior, and so on; but I shall refer to this question later in connection with the nature of the internal developmental factors.

Natural science aims at clear and unambiguous formulation of demonstrable fact. But nature herself sets limits to this ambition. Experience has shown that formulations which are valid on one scale of observation are inapplicable on another scale. We see this in the transition from large-scale mechanics to quantum mechanics, where we pass through an intermediate region where either method of formulation may be applied and neither fits the experimental facts with precision. Such an experience illustrates the important truth that any formula, scientific or other, is applicable through a certain range only; it is never more than partly realistic. Is there indeed any formula that fits with complete exactness the real "facts" of nature? I mean the independent things which exist in their own right, those which we often call existential objects? A much discussed problem is, how far can existential objects be represented truly by logical or mathematical objects and their combinations? The history of logic and mathematics has shown that if we make the rules of procedure exact and unambiguous and agree on the meaning of terms, we can make constructions and derivations which meet any test of consistency. Statements so derived are "true," since in this realm consistency is equivalent to truth; deductions from rule are inevitable and meet with universal assent; no one denies the multiplication table or the tables of integrals. But the fallacy enters when we expect existential nature to conform completely to schemata of a purely formal or logical kind. Any close observer comparing stated truth with immediate fact always finds insufficiency or discrepancy. Nature has a habit of slipping away from too

rigid formulation; this is its "fluid" quality. Nevertheless, fluids have laws and we may be sure that Heracleitus himself depended on these laws. No one who appreciates the stability of that continually flowing, burning, metabolizing system, the living organism, can be unaware of its strict dependence on modes of action and transformation which have a corresponding invariance or stability. It is clear that without such stability of process the evolution of living beings would not have been possible.

Scientific formulae are statements of stability; they are concise descriptions of the invariant factors or conditions which we find present in even the most variable facts of nature. Exact measurement shows that continually changing systems no less than static systems are subject to constant rule and exact formulation. Motion, radiation, chemical action all have their constant characteristics. Nevertheless, it is well to avoid overrating this stability or regarding it as absolute. The true realist will always take formulae with a certain tolerance or grain of humor. This can be done without undervaluing them; they are indispensable tools; yet they remain tools, of human manufacture, approximations, adapted to the human scale of vision and comprehension. It is true that natural existence often runs surprisingly true to mathematical form; yet we realize now that it is a mistake to expect perfect agreement between the formal and the existential. This refractory or unpredictable quality of the existential is never more apparent than in the phenomena of life.

And this brings me closer to the special topic I wish briefly to discuss. I have paid tribute to the value of physics as a method of characterizing the external world. Such tribute has been usual with physiologists. Physical concepts have been regarded as the foundational concepts on which the structure of a scientific biology must be built. If we agree that natural science is the formulation of the constant features or regularities of nature, and also a statement of the dependence of its details, however diver-

sified, on definite principles having general application, then the fundamental problem of a scientific biology may be put thus. Do living beings, while conforming to physical rule, owe their existence and special character to other rules of action of a kind peculiar to themselves—or at least exemplified chiefly in themselves—rules which are not taken into account in the purely physical analysis or characterization of life? And if so, what are these special rules?

It has long been debated how far the phenomena of life are representable in terms of physical models. For some time the orthodox biological point of view has been that physiology is a branch of physico-chemical science. Lately, however, the tide of opinion has swung away somewhat from exclusively physical conceptions of the living organism. There are various reasons for this, partly connected with the advance in psychological science. Physics is in its nature spatial representation; its subject-matter is an external world, consisting of entities and factors with spatio-temporal interrelations. Physiology is also an exteroreferent science; it conceives life as complex physics, as an externality which, however complex in kind, is bound to yield its secrets to persistent physical analysis. The difficulty with this conception, from the standpoint of a general biology, is that it represents only one side or aspect of life, namely, the external. There is also its inner side, its intrinsicality or immediacy, which is a matter of direct experience and hence has priority over the externalization and physical analysis of orthodox physiology. I need not enlarge on this. Every man is aware that his inner life has features which are not spatially representable, or indeed representable (symbolizable) in any terms. No descriptive combination of concepts, however ingenious and exact, can be a substitute for any strongly felt immediate experience. A pain is what it is—pure affective experience. Its scientific description is no consolation to the sufferer. We can not describe it, we can only point to it. Similarly, no one can

describe the exertion of will; it has to be experienced; the willing agent is directly aware of a kind of activity not representable in physical terms. All we can do is to call attention, verbally or otherwise, to the experiences themselves. These have terms or qualities common to all human beings, perhaps to all experiencing subjects other than human. There is a character of ultimacy about these two types of experience—pure feeling, pure volition. Certain ultimates seem unanalyzable, like the concept of energy in physics. We are satisfied for the present if we can analyze complex experiences into such ultimates. The best we can hope for, scientifically, is that both physiological and psychological analysis, if carried far enough, should converge to the same ultimates.

I am reminding you of the difference between direct experience and description. It is not necessary to be a mystic in order to recognize the limits of description. Now science is essentially exact and dependable description. Description becomes explanation when we reduce complex phenomena to familiar characters or qualities and familiar modes of interconnection. To describe means substituting concepts and their combinations for the reality itself. Scientific concepts are general terms; they relate to the constant or repetitive aspects of nature. Science is generalization. It is not interested in the single experience as such. Any immediate experience has in it something which is unique or individual—an existential nature of its own which is not repeated and is therefore not representable in general terms. This is why many psychologists agree that an introspection has no scientific value; and it is often said by scientific men that anything which is not measurable—*i.e.,* not made up of constant elements which can be summed or combined—is outside the realm of science. Although this statement appears extreme, we must acknowledge that there is a sense in which exact science is applicable to all types of experience, since we observe that any single item of experience (any particular), however unique it may seem, has in it

certain components or elements which are common to other particulars, *i.e.,* which are stable or constant. Only in so far as it contains such elements is it describable and hence a subject for science.

Our question is: are there constant elements or modes of action in living organisms which are not present in non-living nature? Life appears to external observation as complex process centering in certain highly organized physical systems. Synthetic activity and integration are the chief features of this process. Can we characterize in exact terms those factors peculiar to life which are responsible for its unique ability to transform random distribution of materials and energy into the special and closely integrated distribution characteristic of living beings?

We agree that development is the fundamental vital activity. In development we see new structures, qualities and activities, based on new types of ordered arrangement, emerging as a result of the conjunction of materials and energy taken from the environment. Each ontogeny illustrates that creativity which Claude Bernard and Whitehead have described as the essence of life. What does analysis indicate as the primary or essential factors in this synthesis?

One main conclusion, on which again I think we all agree, is that the special creativity shown by each species in its developmental cycle is the expression or outcome of factors which are *internal* rather than external. The external factors of development, while indispensable, are conditions under which the internal determinants act, rather than determinants themselves. Under the same environmental conditions each germ pursues its own specific cycle of transformation. Even in adult organisms we can account only imperfectly for their characters through a consideration of the properties and external connections of their observable parts. The impulse or activity which expresses itself in development is one which is directed from *within*. Outflow of material and influence

from a center—or, as development advances, from secondary centers—dominates the constructive process. In this respect the living organism offers a definite contrast to an artificial machine, such as a steam engine, where fixed and readily observed external connections account completely for the special kind of activity shown. It is true that developing germ and artificial machine have certain conditions of action in common. In any regularly repeated sequence of events some stable controlling condition is required; this is furnished by factors, or a combination of factors, whose essential character is invariance or constancy. Experimentally we find that the factors of development show a quantitative constancy, like those of other regular natural processes. But what seems increasingly clear is that the methods of classical or large-scale physics are insufficient for the kind of analysis required. The remarkable feature about the living and developing organism—and in a sense an organism is always developing—is that a spatially minute or microphysical influence appears always to be predominant; this influence is exerted by, or through, submicroscopic entities having the physical character of complex molecules. Fundamental among these are the nuclear molecules or molecular complexes which we call the genes.

We come now to more special physiological considerations. Just how the genes control the course of ontogeny is not known. Apparently this control need not be continual; this is seen in the fact that cytoplasmic activities (even cell-division in some cases) may continue for some time after the removal of nuclei. The influence is exerted indirectly—primarily by a control over constructive metabolism. In the presence of specific genes certain synthetic reactions are reduplicated, apparently indefinitely; *e.g.*, special reaction products, such as pigments, appear constantly in the presence of certain genes. In some way the genes act, directly or indirectly, as centers of reduplicative metabolism, and their own substance is included in this reduplication. Their own stability is re-

markable; and their controlling rôle in heredity depends on this stability. It is to be noted that ultravirus and bacteriophage molecules show a similar reduplication during the growth of the animals or plants which they infect and whose structural and physiological characters they influence in specific ways; and in these respects, as well as in their molecular size, they resemble genes. The conditions of this reduplicative type of metabolism are not clear; the analogies of autocatalysis and crystallization, while important, seem insufficient. The fundamental fact to be noted here, however, is that the ultimate determinative events in ontogeny are chemical reactions; hence in any far-reaching analysis we are brought to consider the general physics of chemical reactions, as natural processes of a special kind. At present we regard these processes as depending on transfers of electrons or atoms or atomic groups between molecules, or in some cases within single molecules. The properties of a compound are referred to the nature and special interconnections of the atoms. But atoms are not physical ultimates; and their own properties are referred to the nature and interconnections of their component units—electrons, protons, neutrons. Again, the constant properties of these units imply a corresponding constancy of inner constitution, and so on; in brief, we see a vista of determinative influence (exerted from within out) receding into elements which become successively smaller and smaller on the spatial scale. Subdivisional analysis of this type would seem to have some limit, but this limit does not seem to have been reached as yet. The idea that space is infinitely divisible is a definitional or analytical idea to which actual existence need not necessarily conform; permanent indivisible quanta might ultimately be reached; but something internal would have to determine the properties and behavior of these units. Whatever the final components may turn out to be, the general cosmic stability requires that these elementary units should also be stable.

The scientific and largely experimental problem is concerned with defining in exact terms the stable factors and conditions which are responsible for the regular sequence of changes shown in the typical ontogeny of any species. We are struck chiefly by the constancy of these processes and the tenacity with which they hold to a normal course. When we refer a part of this regularity to "regulation," we do not mean that we are satisfied with a verbal reference merely; we seek experimentally to isolate the factors which determine the constant interconnections between successive stages and impart unity to the whole sequence. Evidently the "organizer" acts on an organizable; what experimentally substantiable statements can we make regarding this latter? There is little satisfaction in reading into the germinal protoplasm the properties we require for an analytical "explanation" of development. Exact factual knowledge is essential, and we have a morphological embryology and the beginnings of a metabolic embryology. We recognize that each stage as it is reached furnishes the foundation for a process (or processes) leading to the next stage; in this sense each stage may be called an organizer for the next stage. Finally, an adult stage is reached, although this is far from static, even at its limits of growth, since (*e.g.*) it still retains the power of regulation.

Recent progress in physiology and biochemistry has made it clearer than before that whatever occurs at each stage of ontogeny is a function of its chemical as well as morphological constitution. Broad anatomical differences, like sex differences within a species, may depend on single hormone influences; these act ultimately on cellular processes. The protoplasmic substructure of the organism is a product of the synthesis and orderly distribution of definite chemical compounds, especially proteins; these together with other structure-forming materials are deposited in definite spatial positions; in both the synthesis and the distribution a central or nuclear influence seems predominant. The biochemical and the

morphogenetic sequences are closely interdependent; metabolism forms structure and structure controls metabolism. The microchemistry of the system is of equal importance with its cytology and histology; but the unity of the whole developmental process is scarcely made more intelligible by such considerations, even though in principle we recognize that systems of the same initial constitution, placed under similar external conditions, must pass through similar cycles of transformation.

Let us now look at the problem from another angle. Past history has a special significance for living organisms, as Darwin first showed clearly; Driesch and more recently Donnan have reemphasized this. Complex ontogenies have not come into existence suddenly: behind each lies a prolonged evolution. The biological analogy of memory has been evoked to "explain" ontogeny. Life is based on habit; and, as Whitehead has expressed it, "Cause, repetition, habit are all in the same boat"; the common characteristic is stability of process, conformity of action to fixed rule. The constant ontogenetic habit of the developing egg has its analogy in any fixed habit of the adult. In both cases the same cycle of action or transformation is exactly repeated; there is constancy or stability of sequence. Underlying this stability we infer a corresponding stability of controlling conditions. We have seen that in any complex physical system the only way of securing constancy of action is through constancy of structural conditions. In the case of organic habit this structural stability has been attained through frequent repetition of the same action. Experimentally we find that repeated voluntary actions become habitual and finally automatic; and we infer that the accompanying neuromotor activity leaves behind it some structural or constitutional modification, which becomes more the firmly fixed (up to a limit) the oftener the action is repeated. The action lays down its own record, and the formation of this record follows definite quantitative rules, shown graphically in learning curves. Learning, however, is

only one example of a natural process in which repetition of an action facilitates its recurrence. The same condition is exemplified in many non-living systems, as when a stream cuts out a water course, or an automobile engine is broken in.

Hering described memory as a universal character of living beings, and he included ontogeny among its manifestations. Is there any value in this identification? or is it simply one more instance of the many fallacies, based on misapplied terminology, which have played such havoc in human thinking through the ages—and do so still? If —or when—we say that the egg "remembers" the cycle of formative change leading to the adult stage, we are implying that the constancy of this sequence is founded on physiological conditions identical in kind with those which enable a man to perform again and again a complex constructive act which he has learned. What, if any, factors have the two processes in common? The general or verifiable fact is that the germ of any species, under normal external conditions, repeats the same sequence of transformation over and over again. We infer that there is some permanent feature of germinal structure or constitution which makes this possible. According to evolutionary theory this special constitution has been acquired by slow degrees in the past, partly—if indirectly—under the influence of environmental conditions. Once having been laid down, this organization persists and forms the condition for a constant or uniformly recurring type of formative activity. As thus conceived the similarity of ontogeny to the repetition of a learned or remembered routine becomes obvious. The more general class of mnemonic modifications includes both.

What can we say regarding the general physical basis of memory and mnemonic modifications? Do we find phenomena of an analogous kind in the non-living world? The evolutionary doctrine implies their existence; but can they be demonstrated? We may point to special artificial devices like phonographs or other types of recording and

reproducing apparatus, like the recent devices, based on electrolysis, which reproduce the form of a current passed through an electrolytic cell; but these analogies are not sufficient, the proof should go deeper. Such mechanisms are merely special exemplifications of a wider natural principle or law of conservation; this principle is the simple but fundamental one that the present is built upon—"inherits from"—the past, and that the past has the special character of stability or unalterability. The rule of causality is one form of this principle. What it implies is that all natural occurrences have a cumulative or additive character; every event leaves a permanent impress in nature. Accordingly, each stage in any localized sequence of events is a record of preceding stages and lays the foundation for succeeding stages. The records may be overlaid, but in some sense they remain as permanencies. With the aid of amplification and photography we now make permanent records of a fluctuation of potential in a single nerve fiber, or of the transfer of a single electron in a Geiger counter. Can we assume that in the absence of this special apparatus such an event leaves no trace in nature? The physical doctrine of conservation implies some permanent alteration, although the immediate effect may be dissipated so as to be inappreciable at the special locus of any observer.

A simple rule applies here. If the effect of any action is to persist as a record, demonstrable to an observer, part of its energy must be applied in such a way as to cause a permanent and definitely localized change of state in some durable material that can be examined later. Any recording material must therefore combine plasticity with durability. In general such material is solid material. The physical character of solidity is coherence, elastic resistance to the displacement of parts; in general we regard solidity and the persistence of special structural characters as one and the same property. Are mnemonic records, then, or the organizational records latent in the germ, to be regarded as records laid down in solid mate-

rial? At present it is customary to consider "solid" as equivalent to crystalline or microcrystalline; optical and other evidence shows that crystalline structure depends on the coherence of similar molecules in similarly oriented aggregates. Fine-grained or ultramicroscopic structure is referred to the special geometrical characters of the molecules; these are regarded as retaining definite shape and dimensions, at least within narrow limits of variation. Is there any meaning in regarding molecules as solid structures? Structural formulae do in fact represent molecules as solid in the sense of consisting of stable parts, atoms, which cohere in a definite pattern; these constant interconnections are regarded as determining the special properties of the substance. The permanence of complex molecules like protein molecules is a permanence of structural constitution, in the sense of definite and stable interconnections between the component subgroups. If such molecules are sufficiently large and complex, and also have what correspond to plastic properties, they may serve as tablets on which records may be laid down. Subgroups may undergo substitution or shift their relative positions, with corresponding changes in the properties of the molecule as a whole.

At present the evidence indicates that it is this combination of stability with molecular complexity, in compounds controlling the general course of synthetic metabolism, which determines the special character and the reduplicability of the developmental process. The genes are regarded as consisting chiefly of complex protein molecules, and much is now being made of their analogies with ultra-virus material. The virus material is protein of high molecular weight and crystallizable; it can be shown experimentally that its presence determines definite metabolic and formative changes in the infected animal or plant. Changes induced in the virus by physical agents like radiation may alter the character of the changes which it induces in its host. There is here an evident analogy with mutation. In the related field of immunology it is

known that slight substitutional or configurational changes in proteins may affect definitely their antigenic character, *i.e.*, their influence on constructive metabolism. The special action of enzymes is also dependent on special molecular configuration. It is reasonable to assume that similar slight changes in the proteins of genes will have analogous effects on their properties as determiners in development.

The conclusion has accordingly been drawn that protein molecules of a complex type which are exactly reproduced or synthesized in the metabolism of an organism constitute the fundamental determinative factors in any special ontogeny. These complex molecules, like simpler molecules, are regarded as depending for their specific properties on the permanent properties and interconnections of their component atoms. It is evident, however, on fuller consideration, that a more complete analysis would have to account for these properties and interconnections; again, physical analysis does not stop with the atoms, and we refer the properties of atoms to the permanence of their component electrical units and the special interrelations between these. The electron itself is a subject for further analysis. The general picture is one of stable elements within stable elements (like a Chinese box), the properties of the larger or inclusive components being determined by the special properties and interconnections of the included components. The properties of the final included components would be the fundamental ones. But, as we have already seen, there can be no finality here, since anything spatial or extended is assumed to have an interior, with properties depending on the constitution of that interior. Hence a purely spatial or physical analysis will not reveal the final organization; there is always the difficulty of indefinite regress.

Any composite stable natural unit is called by Whitehead an organism. Evidently a prerequisite to organization (in this sense) is that the smaller components shall be stable and retain constant interrelations within the whole

system. The problem of the factors of stability of elementary units thus inevitably arises. Why does an electron cohere, instead of disrupting with its inner tension? Why does nature concentrate mass and energy in discrete atomic units? Also what is it that determines the special activity of the individual units—since the properties of the whole depend ultimately on the summation of these internal activities? In the living organism is there a special whole-making factor? All these questions have a relevance to our problem, however difficult they may be to answer at present.

If we say that life depends on some ordering condition or principle active within nature, we are likely to be accused of mysticism, or at least of substituting verbal for factual explanation. But order and constancy, both of static character and active manifestation, are natural facts, in no sense peculiar to life, as the physical sciences show. We find that the kind of order exhibited by living beings differs in its special character from the order of non-living nature. Not that it is independent of the mathematical and physical order; obviously it requires that order and is based on it. Yet nothing is to be gained by ignoring what is peculiar to life as a special natural phenomenon. I have already indicated what seems to be its distinguishing characteristic. The vital impulse or activity imposes order, unity and organization on materials and energies which otherwise would have a haphazard and incoherent distribution in nature. These converge to form the organism, the convergence being presided over by an ordering and unifying condition of a specific kind. This statement is general and purely descriptive. Let me give a concrete illustration. If we sterilize a culture medium and then reinoculate it with a specific microorganism, or if we sterilize a banana and reinoculate it with Drosophila, we know from repeated experience what happens. A definite organizing sequence is initiated, centering at the germ and leading to the synthesis of the specific plant or animal. Without the inocu-

lation the food materials retain their random distribution, *i.e.,* one having no relevance to the special character of the living being that later emerges. We introduce the germ and the living organism is synthesized. It is like reassembling the scattered fragments after an explosion; the required movements can not be casual but must be directive, *i.e.,* subject to a definite integrative type of control. Under this control the dispersed elements converge to find their proper places in a unity having a constant and specific pattern or organization. The terms convergence and localization merely define the most general features of the process. The special requirements for reassembling a complex system after dissipation are formidable; some of them may be made optically visible in a reversed movie film, *e.g.,* a slow-motion picture of an explosion. Precision of adjustment, selection of highly definite movements and exclusion or compensation of purely random movements (particularly in the final stages) are what we observe. In the film we know that the end stage is already in existence at the beginning of the sequence; we merely reverse the temporal order of the individual pictures; but the illustration shows at least that in order to effect a definite synthesis from randomly distributed parts, the motions of these components must follow a directive or predetermined course; *i.e.,* some stable condition determining this course exists in advance. The inference follows that an analogous directive action, under stable control, must underlie the vital synthesis.

The synthetic processes of development exhibit characters which appear to be the reverse of those activities of diffusion or expansion, dependent on random motion, which usually underlie processes of dissipation or disintegration. Hence many biologists have inferred that in development or any other directive vital action the second law of thermodynamics (an expression of uncoordinated molecular motion) is locally or temporarily abrogated. To avoid this conclusion other biologists, of the "mechanistic" school, are prepared to go to almost any lengths.

But is the issue really a controversial one? The second law is a law of macrophysics, not of microphysics; it does not apply to single molecular actions. In many natural events a large-scale randomness may be quite compatible with a small-scale directiveness, as we see in many human affairs; with large populations the curves of vital statistics often conform closely with probability curves of a type applying to random events in general. Yet we know that, individually considered, the actions thus summed up may be voluntary and directive. In the developing organism it seems clear that the primary directive influence, whatever its nature, has its application on a microscopic or ultra-microscopic scale. It acts as an individual rather than a statistical type of occurrence. The conclusion that the developmental process is fundamentally directive in character is admitted in some form by all biologists. To expect the random materials of the nutritive environment to reach their final destinations as components of the highly organized living system without some directive guidance would be like expecting a ship to reach its port without steering. The problem is to find the basis of this directiveness.

The usual physiological attempt is to refer the vital ordering factors in development to ordering factors of a more general type demonstrable in non-living physical nature. While admitting the value of this procedure, we may criticize it as insufficient; relied on solely, it introduces restrictions that may prevent a satisfactory solution from being reached. Physical science deliberately abstracts from the possibility of teleological intervention in natural events; biophysics and biochemistry follow this tradition. No doubt it is true that the forms of order established in the physical world control or limit the possibilities of vital action; nothing is vitally possible which is not physically possible. Physiological analysis shows vital action as relying throughout its whole range on the constants of physical action. But to regard life as "nothing but" complex "physical" action is a speculation of

too sweeping a kind. Such a belief easily hardens into a dogma that hinders unprejudiced investigation.

Thus to return to morphogenesis, there is the temptation, strong to the simplifying type of mind (and all scientific minds are simplifying), to regard the transformation of banana into Drosophila as occurring by some kind of crystallizing process, centering in the genes, and extending by some further process of interaction to the cytoplasm and its products. If viruses may form crystalline aggregates, why not the specific germinal substance—particulate material of similar dimensions and in some respects comparable properties? This hypothesis would place a non-vital type of morphogenesis at the basis of the vital. We may admit the experimental truth lying behind the view that the formative factors in crystallization and in morphogenesis are largely the same. Experimentally we find that the x-ray diffraction patterns of organic structures show a regular microcrystalline structure. It is a fair inference that without the formation of microcrystalline deposits, having a specific structure dependent on the chemical configuration of the molecules, there could be no constant protoplasmic structure. If aggregates of similar protein molecules did not fall automatically into constant alignment and form, it is difficult to see how there could ever be a constant morphology in the biological sense; and without a constant morphology there could be no constant physiology; the vital development would not have been possible.

Such considerations show how important the purely physical analysis of the living organism may be. Yet to suppose that nothing more than the tendency of special compounds to segregate and crystallize is needed to account for organic form would be to fall into a fallacy of over-simplification. The special disposition of the parts in the broad unity of the active and finished organism—not merely the characters of the microcrystalline deposits—is what we have to account for. The character of the whole can not be adequately explained by reference to the

characters of the minute parts. Some broadly active synthetic and unifying principle is required. Here I use the word "principle" for want of a better, as signifying something stable and foundational whose regulative influence is everywhere present in the organism. How can we conceive this vital principle?

My own conviction is that no merely physical conception is sufficient. But I say this without prejudice to the physical methods of analysis in biology. These are indispensable, as having reference to the externally demonstrable and stable factors always present in organisms. Unlimited progress in this field is to be looked for. Especially striking have been the results of recent work on the physical chemistry of proteins; and in conclusion let me refer briefly (following the example of my recent predecessors) to some of the bearings of this work on our problem.

If, proceeding on the physical plane, we refer what is specific in each living animal or plant ultimately to the chemical specificity of its proteins, we have then to inquire how the special molecular constitution of these compounds (*e.g.*, of the genes) has been attained, and how it can determine with such uncanny precision the course followed by the developmental synthesis. While we can not trace the connection between a specific protein configuration and the physiological characters of the adult organism, it is interesting to note that we have already evidence of definite chemical relations existing between protein structure and the structure of sterols and related compounds, including growth-influencing hormones such as the sex-hormones. The relations between metabolism and morphogenesis will undoubtedly become clearer as our knowledge advances in this field.

At this point, admitting that the detail is beyond us at present, we may fall back on a fundamental guiding principle of experimental science, namely, that every reproducible phenomenon is based on stability of conditions. A complex recurrent process like development must start

with a correspondingly complex set of stable conditions. At present the indications are that this combination of stability with complexity is furnished by the specific proteins of the germ, particularly the nuclear proteins of (or in) the genes. These appear to be mainly nucleo-protein in nature. I have already referred to the analogy between viruses and genes; the large molecular (or micellar) size of the viruses is a fact of much significance for the physiology of development. The ready displacement of nuclear chromatin in the ultracentrifuge indicates a high sedimentation constant for this substance; and the recent work of Northrop and others has shown that bacteriophage and viruses consist largely or mainly of nucleoprotein molecules (or micelles) of many millions molecular weight. If protein films or lattices, having the intricate network-like structure recently described by Dr. Wrinch, hold a key position in the nuclear metabolism, the metabolic processes which they control will have a corresponding complexity, in conformity with the special chemical and structural characteristics of the layer. These characteristics are fixed by conditions which ultimately are physical and geometrical. Changes in the spacing or chemical character of the R-groups or purine groups will alter correspondingly the specific character of this influence. The production of mutations by radiation may have some such physical basis. We may compare the conditions with those observed in immunological reactions, where specific changes in antigenic character result from substitutional or positional changes in the protein molecules. Antigenic reactions have a special (if indirect) interest for the physiology of development, since they show how minutely selective the metabolic influence of a configurational pattern may be. Enzyme reactions offer similar analogies. The ability of proteins to form complex surface patterns, at once stable and subject to modification under changing conditions, may be the basis for the fundamental part which these compounds play in life processes. They appear to possess the required com-

bination of structural complexity with stability; they also show plasticity, or minutely graded modifiability without loss of characteristic identity. The chemical influence of such a definitely patterned mosaic will be complex, with a selective action at each local position. Its surface may be regarded as a catalyzing surface; through its special structure trains of influence or control are guided into definite channels fixed by molecular constitution; the course of constructive metabolism and of the dependent formative processes is thus stabilized. This influence is all-pervasive in each individual, since each nucleus has the same set of genes. With such an internal molecular basis for unity and stability the modifying effects of external factors will be restricted, as well as regularized.

The conditions which I have just indicated are stable conditions; but we must not overlook what remains after all the chief peculiarity of living organisms—the presence of spontaneous or creative activity, manifesting itself in evolution or in individual behavior. In non-living nature the tendency of activity to pass beyond routine is much less evident, while apparently not entirely absent. Creativity always has a background of stable organization, although this organization, if not well contrived, may lead the creative impulse into erratic courses; of this there is ample evidence in organic evolution, as well as in individual life, animal and human. Science, however, as science, is concerned with the stable or verifiable characters of organisms; it is these alone that biologists may hope to understand by reference to physical models. The novelty-producing or creative character of living beings must be referred ultimately to other factors, equally deep-seated and equally characteristic of natural existence. Of these factors science can at present give no account; can it ever give an account? The creative is that which escapes or transcends rule; but what is not in accordance with rule lies outside science; in an evolving universe all the rules are not yet made. Biologists need not be disturbed by this consideration; the scientific path remains

clear, and its outlook is fuller of promise than ever before. There is an incomparably rich field in the determination of the natural constants of vital phenomena. These constants are the basis on which the vital organization has been built; and our scientific control over life in all its manifestations will expand in proportion as our knowledge of this organization becomes more exact and deeper. For this advance we look with confidence to the novelty-producing and creative activity of our investigators.

SUMMARY

The main purpose of this general or theoretical address is to emphasize the concept of life as fundamentally a process of synthesis and integration. In the organizing process materials randomly distributed in the environment are assembled and unified to form the living animal or plant. This process has as its prerequisites (1) constancy in the properties and modes of interaction of the materials, and (2) constancy in the activity of the special vital factors which control or direct the integration. These vital factors are not to be identified completely with purely physical factors, although they are dependent for their effective operation on the constancy of the physcial units and physical modes of action. They appear, for example, to include directive factors acting oppositely to simple processes of diffusion ("anti-diffusion factors"). A fundamental characteristic of the vital factors seems to be a physically indeterminate "creative" side, shown in a tendency to depart from routine and to produce novel action or organization. This tendency is seen in evolution as well as in individual life. At present, however, the stability of living organisms (dependent as it is on the stability of many interacting processes) is to be referred mainly to constant factors many of which can be physically defined. Living beings are the outcome of a prolonged historical development or evolution; their organization is a record of factors acting progressively and cumulatively in the past. Hering's comparison

between memory and ontogeny is apposite here. The mnemonic records laid down in the nervous system during individual life have their analogies in the records laid down in the germinal material during the evolution of the species. Permanent structural characters always lie at the basis of any permanent capacity for carrying out complex trains of activity; this principle applies both to individual memory and to "germinal memory." The present evidence indicates that the specific characters of a given ontogeny are to be referred for their ultimate physical basis to stable and specific types of molecular structure present in the germ at the beginning of development. This structure (developed by degrees in the evolutionary history of the species) appears to be that of certain nucleoproteins in the germ nuclei, *i.e.*, in the genes. The analogies, chemical and biological, between genes and ultra-viruses are pointed out, and there follows a brief discussion of the possible relations between protein structure and the determinative rôle assigned to genes in development. By virtue of their large molecular size and complex configuration (consisting apparently in a network-like arrangement of amino-acid residues and purine groups) the possibilities of minutely graded diversification in the germinal proteins are unlimited. These compounds hold a controlling or key position in the metabolism of the protoplasmic system, and apparently they control or stabilize in a specific way the metabolic reactions which underlie the formation and distribution of the structure-forming compounds. The course of development thus depends for its stability and its special character on the specific molecular (or micellar) structure of the gene proteins. These are reduplicated automatically in each cell-division, and normally are passed on unchanged from generation to generation. But if their structure is altered, *e.g.*, by slight positional or substitutional changes in the determining groups, corresponding changes in the course of development may result (*e.g.*, artificially induced or spontaneous mutations).

DARWIN'S THEORY OF SEXUAL SELECTION AND THE DATA SUBSUMED BY IT, IN THE LIGHT OF RECENT RESEARCH

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INTRODUCTORY

DARWIN's theory of sexual selection was of the compound deductive-inductive type. Deductively he postulated: (1) that under certain circumstances there would occur a struggle between males for mates, and that the characters giving success in such a struggle would have sexually-selective value and would be perpetuated irrespective of their natural-selective value in the general struggle for existence; (2) that these characters would be of two main types, (a) those subserving male display, (b) those subserving combat between rival males, and that such characters could not be evolved except under the operation of sexual selection as defined by him. With regard to display characters, he further deduced a rudimentary esthetic sense in females, and also a process of female choice as between rival males.

Inductively, Darwin proceeded to collect examples of actual display and combat and of characters which he supposed to subserve either of these two functions, and to use these as evidence that a process of sexual selection had occurred.

He was inclined to ascribe a display function to all bright colors except a few concerned with warning and with recognition; even when they occurred in both sexes, he postulated their origin in the male through sexual selection, followed by their transference to the female by the operation of the laws of heredity.

This method is not, as has been asserted by some critics, a circular argument, but a perfectly justifiable procedure if the deductive analysis is correct and if certain precautions are used in collecting data for the induction.

Since Darwin's time, the situation has changed so that we can see that his views need considerable emendation on both the deductive and inductive sides.

In the first place competition between males for mates, accompanied by any form of female choice, is not the common phenomenon postulated by Darwin, but apparently confined to the relatively few species practising polygamy or with a high excess of males. In most monogamous birds, display begins only after pairing up for the season has occurred (Howard, 1907–14, Huxley, 1923). In general, male secondary sexual characters subserving display or combat fall into the same general functional category as accessory male characters such as copulatory organs, or primary male characters such as those of the sperms, which were not regarded by Darwin as having been evolved by sexual selection: *i.e.*, they are adaptations promoting the union of the gametes. The term *epigamic* (Poulton, 1890) may thus be applied to them in an extended sense. All those characters which exert their effects via the distance receptors of other individuals, of the same or other species, may be called *allesthetic* (Huxley, 1938).

In monogamous forms, all such epigamic characters can thus be regarded as owing their origin, at least in the main, to natural selection, but of a sex-limited nature.

Darwin further failed to draw a general distinction between inter-specific and intra-specific selection, although in sexual selection, as defined by him, he gave the first example of intra-specific selection promoting individual success without advantage to the type.

Criteria for Allesthetic Characters of Various Types, His criteria for display-characters were quite inadequate. The only fully safe criterion is the direct one, of observation showing that display occurs and is directed at an individual of opposite sex, and that the character (bright color and/or special structure) is more prominent in display than normally (see also Fisher, 1930). Even

when these criteria are satisfied, it is frequently found that the same characters may have other functions, of which threat (to rivals of the same sex) or sex-recognition (by members of either sex) are the commonest. In such cases the character, though sometimes employed in the same way in both functions, is usually employed differently in relation to its different functions. Indirect criteria, however, may still be applied, but with a lower degree of assurance.

Many conspicuous characters (bright colors, songs, special structures or modes of behavior), to which Darwin assigned display function, have now been shown to have other functions (see Huxley, 1937, for examples). These include: (a) deflection of predator attack, notably inter-individual deflection, from more to less biologically valuable individuals (see Heinroth, 1938: Bulwers's Pheasant); (b) warnings (to enemies of other species) of noxious or dangerous qualities; (c) false warning (Batesian mimicry) and bluff; (d) recognition characters (not only between adults, irrespective of sex, but between the sexes and between juveniles and adults (see Molony, 1937); (e) threat (to rivals of the same species and usually the same sex) of combative impulse and prowess: see Hingston, 1933.

Of these, that of threat characters includes a large number, probably the majority, of the cases adduced by Darwin as subserving display and therefore evidence of the existence of sexual selection.

Threat characters are of several distinct types (A) subserving distance-threat (recognitional threat). Such characters advertise the presence of a potential combatant to rivals at a distance and often may save him the exhaustion and danger of actual combat by deterring the rival from intrusion (deer antlers; bright colors of male lizards—see Noble and Bradley, 1933; bright colors and songs of male territorial birds after pairing up; *cf.* similar economy-function of warning characters, *e.g.,* wasp's

color-pattern, rattlesnake's rattle). They frequently combine this function with that of distance sex-recognition, by advertising the presence of a potential mate to unmated individuals of the opposite sex (bright colors and songs of male monogamous birds before pairing-up has occurred; Howard, 1920). (B) Subserving short-range threat. (1) By the revelation of striking patterns, etc., advertising their possessor as a potential combatant. Characters of this type will be of the same general type as distance-threat characters, but on a smaller scale and usually confined to the head, face and throat; since these will be conspicuous in preparation for combat (*e.g.,* facial patterns of many male birds, white eyelids of male Gelada baboon, etc.) these may be grouped with those subserving distance threat as recognitional threat characters. (2) By the revelation of actual weapons or combative prowess, as in baring the canines by snarling, enhancement of apparent size by bristling of hair, etc.; these may be called preparatory or symbolic threat characters. Short-range threat characters may, like long-distance ones, obviate the need for actual combat, and when in the form of pattern, may also subserve the additional function of sex-recognition (''moustache'' of male flicker, etc., see Noble, 1936; Noble and Vogt, 1935). Threat characters may also serve as warnings to enemies of other species.

Observation confirms deduction as to the general characteristics to be expected of conspicuous allesthetic characters, according to the functions they subserve. (a) Characters subserving recognition and recognitional threat have the function of arresting attention. They will accordingly require to combine conspicuousness with distinctiveness (see Lorenz, 1935).

The degree of distinctiveness (for the species, in one or both sexes) will be high when it is biologically desirable to avoid confusion with members of other species or of the opposite sex, *e.g.,* recognition marks of gregarious species with functions of keeping members of the species together

but separate from other species; sex-recognitional characters; recognitional threat characters. The resultant characters when visual will tend to take the form of patterns with a few components of form or color arranged in a striking and distinctive way. Auditory characters will achieve the same end in an equally obvious but less readily definable way. In territorial passerine birds, there tends to be an inverse relation between the development of auditory distinctiveness (song of species with cryptic behavior and coloration, *e.g.*, grasshopper warbler, chiffchaff) and visual distinctiveness (pattern of species with conspicuous behavior, *e.g.*, stonechat, pied flycatcher). When confusion can not easily arise, the characters may be simpler (and therefore less distinctive though equally conspicuous) as in white tails or rump-patches employed as guide-marks in case of danger.

Long-range sex-recognitional and threat-characters will tend to be prominent continuously or for long periods (and not to be revealed only in relation to special emotional states). When visual, they will (like inter-individual deflection characters) take in all or most of the body. When adapted to act at short range they will tend to be on a smaller scale, usually restricted to face or fore-parts, and may sometimes not be continuously visible, but only revealed in relation to special emotional states, such as pugnacity.

Characters subserving epigamic display and symbolic or preparatory threat (and warning) have the function of stimulating emotion. In this category, when visual characters are present, they are always combined with special actions, usually of a striking nature (unlike visual characters concerned with deflection, distance threat or distance-recognition, which are often unaccompanied by specific action). (1) Symbolic threat-characters are concerned with eliciting fear or submissiveness. They will thus tend either to increase apparent size or to reveal or emphasize weapons or enhance the

appearance of anger or combativeness. Distinctive conspicuousness is not called for to any great extent, but rather the enhancement of the formidable quality of their possessor. (2) Display-characters are usually concerned with eliciting sexual emotion in general and readiness to mate in particular. Display actions may sometimes be described as preparatory or symbolic, as when behavior reminiscent of coition forms part of display. In other cases they appear to be expressions of general excitement, as frequently occurs also with symbolic threat actions: if so, they may often have the mixed functions of threat to rivals of the same sex, and sexual stimulation of potential mates of the opposite sex. When visual characters are present they are invariably revealed only or especially by means of the display actions. When special structures (long plumes, etc.) are employed, they are invariably developments of parts that are prominent during display actions: when strongly developed they may mask the original symbolic use of the part.

The most striking fact about visual characters which are used *exclusively* in display (and not also in threat) is that they are beautiful rather than distinctively conspicuous: *i.e.,* the patterns will not be simple schemes of contrasting areas easily recognizable at a distance, but intricate or delicate, adapted to close-range effectiveness, and regarded in human beings as beautiful rather than merely striking. The wings and tail of argus and peacock pheasants and the plumes of egrets and lyrebirds are perhaps the best examples. Thus Darwin's postulate of some esthetic sense in female animals appears to be justified, at any rate among birds. When, as frequently occurs, the same character subserves both threat and display, it manifests a compromise between beauty and conspicuousness.

Employing these indirect criteria to assign biological meaning to striking characters apparently with an allesthetic function, we find among the color patterns or

special structures cited by Darwin as being concerned with display, comparatively few which can in reality be supposed to possess this function alone. Many would appear to combine display with threat and sometimes also with sex-recognition, and many again (apparently the majority of distinctive color patterns) to subserve recognitional threat, either alone or combined with sex-recognition.

Psycho-physiological effects of display and threat actions. Evidence now exists to show that display may induce a psycho-physiological state of readiness to mate, irrespective of any possibility of choice. (Drosophila—Sturtevant, 1915; newts—Finkler, 1923; etc.) In birds, display may synchronize male and female rhythms of sexual behavior (Howard, 1929, 1935; Allen, 1934), initiate physiological changes leading to rapid growth of oocytes and eventual ovulation (Harper, 1904; Whitman, 1919; Huxley, 1932; Marshall, 1936), while threat actions and display jointly may be necessary for reaching the threshold of effective reproductive behavior (Allen, 1934). Defeat in sexual contests or failure to secure a mate may result in lack of ability to breed for the season, or even in death (ruffed grouse, Allen, 1934) or in loss of seasonal epigamic characters (pelican, Steinbacher, 1938; stickleback). The stimulative effect of song on rivals in territorial species is well known, one male often answering another; and Southern (1938a) writes of the ground display of Temminck's stint that "the presence of other birds going through the same display seemed to provide mutual encouragement," the display then lasting longer and being more vehement.

Such effects, when positive, may be additive for members of a group, so that large colonies of socially nesting species may lay earlier and more synchronomously than small colonies (Darling, 1938). This will explain the widespread occurrence of social gatherings for display, even in otherwise solitary species, and the origin of highly socialized reproductive gatherings in species with mating polygamy.

These effects directly promote effective reproduction and need no special category of "sexual selection" to explain their origin.

In various insects, it is necessary for the female to have an abundant protein diet if her oocytes are to mature (see summary and discussion in Richards, 1927). Many cases of food-presentation by the male in insects appear to have this direct physiological effect as one of their functions, although other functions may be combined with this (*e.g.*, general stimulative effect; immobilization of the female while the male adopts a difficult position needed for successful coition, etc. In one case (the orthopteran oecanthus) the food is provided by a special gland on the male's back, and this provision serves to prevent the female from devouring more than a portion of the spermatophore, which in this case provides the protein necessary for ovulation.

Mutual display and "mutual selection." Mutual display, though rejected by Darwin (in favor of unilateral display followed by automatic transference of display characteristics to the female), is wide-spread among birds (not elsewhere: see Huxley, 1923) and apparently has the same psycho-physiological stimulative functions both for coition and ovulation as unilateral display, even when self-exhausting. However, the greater prominence of self-exhausting displays and their continuance long after eggs have been laid, indicate that it also has the special function of acting as a bond to keep members of a pair together during the breeding season. This will be of greater importance when, as is the case with forms showing mutual display, both parents share in incubation and in the care of the young (Huxley, 1914, 1923; Southern, 1938a).

"Ritualization" of display and combat. Many authors have commented on the strange fact of what has been termed the ritualization of actions concerned with display and rivalry, notably in birds. The most obvious cases concern rivalry, where combat often seems to have degen-

erated into bluff or sham fight (see, *e.g.*, references to Selous in Huxley, 1938a, for birds; Noble and Bradley, 1933, for lizards). This may in some cases be due to the advantage (see page 419) obtained by avoiding actual combat. In lizards, at least, there appears to be a negative correlation between the amount of actual fighting indulged in and the degree of development of distance-threat characters, which thus seem to be becoming purely symbolic.

In other cases, however, the advantage probably lies in the psycho-physiological effect of sexual excitement. I would, for instance, suggest that this is the explanation of the constant sparring of ruff and blackcock on their mating-grounds, which all observers agree very rarely develops into actual fighting. In the circumstances of mating polygamy (p. 427), there is little or no advantage to be gained by fighting as regards the obtaining of mates. But the work of Allen (1934) and Darling (1938) makes it clear that such sparring would be expected to have a stimulating effect on the reproductive physiology not only of the cocks but also of the hens which visit the mating-grounds.

A very peculiar case of ritualization is that of certain empid flies (cited by Richards, 1927). The original type of epigamic action in this group is the presentation of actual prey by the male. The acceptance of this by the female facilitates the male in taking up the correct attitude for coition. In some forms, the offering is made more conspicuous by being embedded in a large glistening mass of bubbles secreted by the male, while in still others merely this empty "chocolate box," with or without the addition of a flower-petal or other bright object, is presented. In some of the species of the last type, the female goes through the motions of eating, although there is nothing to eat. Richards suggests that this is an outcome of the chain-reflex type of behavior found in many insects: the motions of eating form a necessary link in the chain of actions leading to coition. Even in birds, some-

thing of the sort may well occur, though no case is certainly known.

Finally, there exists a wholly different type of ritualization, namely, the performance during display, in a purely ritual manner, of actions apparently unconnected with display. The "habit-preening" of the great crested grebe has been carefully described (Huxley, 1914). Similar actions (ritualized rubbing of the head against the back) are to be seen in the mute swan. No satisfactory explanation has yet been offered for this type of ritual action, though in some cases it may prove that the ritualized action was originally employed as the basis out of which the display has evolved.

Correlation of type of display and reproductive behavior with mode of life within a group. This has only been adequately worked out for birds (Huxley, 1923, 1938b). Polygamy and promiscuity promote unilateral male display of striking type, often with extreme development of display structures. Monogamous species (largely passerines), with reproductive economy based on feeding territory, usually develop prominent characters (visual and/or vocal) concerned with distance recognition, subserving both threat and also advertisement to potential mates, with unilateral display restricted to the post-mating period, and rarely with special structures or marked visual characters evolved in relation to it. In treeless areas actions subserving distance-recognition often take the form of display flights, accompanied by vocalization; in wooded or bushy areas usually that of song from a conspicuous perch.

Need for protection from predators is correlated with cryptic coloration and a reduction of conspicuous characters, either altogether or so as to be invisible except during display or threat action. Lack of need for protection of the brooding female (hole-nesters) results in considerable transfer of bright male colors to the female, but without transference of male type of display and threat behavior (for transference in general see Meisenheimer, 1921; Win-

terbottom, 1929b). Need for concealment of the nest usually leads to the performance of epigamic display away from the nesting site (grebes), while it is often performed close to or on the nest when no such need exists (herons, pelicans).

"Reversed courtship" (unilateral female display) is associated with reversal of other instincts (male brooding and care of young) and may be correlated with advantage derived from taking the strain of brooding off females who must devote much metabolic energy to egg-production (relatively large eggs, especially with small forms in high latitudes, *e.g.*, phalaropes). Mutual display is apparently always correlated with general similarity of male and female in plumage and in reproductive functions (both sexes brood and care for young); but the reverse correlation is not universal, many forms in which both sexes are alike in reproductive functions showing an admixture of mutual with unilateral male display, though normally with similar plumage in both sexes, *e.g.*, terns). In such cases, the residual difference in display behavior between male and female appears to be correlated with the need for the male to become temporarily dominant in order that coition may occur (night-herons: Noble, Wurm and Schmidt, 1938). In the absence of such difference "reversed coition" appears to be normal (crested grebe: Huxley, 1914) or frequent (moorhens: Howard, 1929). When food-territory is especially important, the duty of defending territory usually devolves on the male: in correlation with this the male of territorial passerines normally does not brood, though he shares in feeding the young. This sexual difference in behavior is reflected in the complete or almost complete restriction of display and of epigamic and threat characters to the male. When, as rarely occurs, both sexes hold territory in the winter, the females as well as the males develop conspicuous threat-characters (redbreast, Lack, 1938). Obvious deflection characters may be found in the males of monogamous species where

the female alone broods and cares for the young (some ducks, ptarmigans, pheasants). In socially nesting forms, the additive psycho-physiological stimulation of display and threat may have the ecological result of a maximum utilization of relatively few among numerous suitable sites (Darling, 1938).

Polygamy in birds appears to have arisen in at least three separate ways (Huxley, 1938b). (a) Territorial polygamy: from monogamous territorial forms. One male defends several territories (corn buntings, Ryves and Ryves, 1934; weaver birds, Lack, 1935). (b) Family group polygamy, from precocial forms where the male does not brood but remains near the nest and young (some gallinaceous birds, *e.g.,* jungle-fowl and certain pheasants). (c) Mating polygamy (promiscuity), arising from forms with social or semi-social display in special areas (ruff, blackcock, ? birds of paradise).

Correlation of type of display and mating behavior with type and level of organization (see Huxley, 1938b). Two considerations are important: (a) the degree of development of distance-receptors and cerebral organization; (b) the degree to which the sexes are associated in mating and reproduction. The resultant correlations are as follows:

(a) (1) Forms without well-developed visual and auditory receptors will not show allesthetic characters concerned with display or threat.

(2) Forms with developed visual and/or auditory receptors. These may show allesthetic display and threat characters, but the type of these will vary with the specialization of visual and auditory functions, with brain-organization and consequent complexity of behavior-patterns, and with reproductive and general biology and mode of life.

With low cerebral organization and restricted possibilities of behavior patterns, such characters will be confined to indicating the existence of a sexual situation. When eyes are poorly developed, the visual characters involved will be crude and simple (brandishing of large claws by fiddler-crabs); when vision is better developed, these may be more elaborate (display of some male spiders—see Bristowe, 1929), while in the absence of efficient eyes, other senses may be involved (tactile sense via the strands of the web in other spiders).

In indiscriminate carnivores, selection-pressure will act strongly to prevent males being destroyed by females, and will promote either highly developed advertisements of a sexual situation, as in

spiders, or alternatively cryptic actions ("negative display"), as in mantids (Roeder, 1935).

The presence or absence of color-vision may, it appears, safely be inferred from the type of characters known to be associated with display or threat. This has been confirmed for insects, fish, birds and primates (with color-vision), as against mammals excluding primates (without color-vision). The same applies to auditory perception.

Characters subserving distance-threat and visual sex-recognition only appear with high development of visual function.

(b) As regards reproductive specialization, three levels may be distinguished:

(1) Forms in which no true mating occurs, but gametes are freely liberated and fertilization is always external. Here no combat, threat or true display is found. The chief epigamic characters promote synchrony in the liberation of gametes. The most specialized condition seen on this level is the association of numerous individuals in a mating dance or swarm (some polychaetes).

(2) Forms in which mating occurs (*i.e.*, one male fertilizes the eggs of one female or of several single females in successive sexual acts, but no association of the sexes occurs for purposes other than mating. Fertilization sometimes external (most anura and fish), but usually internal. This stage includes most insects, for details of whose epigamic behavior see Richards, 1927.

On this level, epigamic adaptations include characters for discovery of the other sex; for continued prehension of the female by the male; for advertisement of a sexual situation; for stimulating or predisposing the female to coition, including tactile stimulation, auditory, visual and olfactory display, and food presentation (see Richards, *loc. cit.*); for concealment (mantids, Roeder, 1935); for pursuit (social hymenoptera); for mating gatherings; and for combat and threat. This last category is comparatively rare, and is best developed in species with some form of territory (lizards, Noble and Bradley, 1933; some fish, *e.g.*, stickleback), and in some polygamous forms.

Logically, polygamous birds and mammals without family life fall into this category, but historically they represent a specialization of the next level.

(3) Forms in which mating occurs, but the sexes are associated for other purposes also (family life, gregariousness based on the family.

Only birds, mammals and some insects fall into this category.

On this level, epigamic characters must subserve two distinct functions—first, the securing of a mate or mates, and, secondly, the securing of coition. In connection with securing a mate or mates, characters concerned with sex-recognition, distance-threat, threat and combat are often strongly developed. Characters concerned with securing coition are very different in birds and mammals (Huxley, 1923; Marshall, 1936). In birds, mating and reproduction are largely under the control of higher cerebral centers, via emotional states; and here stimulative display-characters are

well developed. In many cases (but in no other group), mutual display has been evolved. As a further result, social display is frequent and leads on to the mating gatherings of some promiscuous forms. The importance of territory in many species promotes distance-threat.

In most mammals, reproduction is more purely physiological, more under the control of lower nervous centers. In connection with this, true display is rare or absent, but male combat, promoting the evolution of large size and of weapons, is frequent. True mutual display, with special epigamic characters developed equally in both sexes, is absent. Male combat leads on to polygamy of the harem type. In primates, reproduction becomes progressively emancipated from purely physiological control, and elaborate threat-characters are developed (Pycraft, 1913), which in some cases may also have display functions. In man a unique type of mutual selection exists in which the epigamic characters differ in the two sexes.

Selective advantages of different type and degree associated with epigamic and threat-characters. All selection connected with sex-limited epigamic characters must be intra-specific, because intra-sexual. In most cases, however, the advantage to the individual (usually male) coincides wholly or largely with the general advantage to the species, since the sex-limited character involved is an intrinsic part of the mechanism for affecting some process necessary for the species—usually fertilization, and sometimes maximum reproductive efficiency. This applies to gamete characters and accessory characters, as much as to those involved in display or rivalry.

The more intense the intra-sexual selection, the more likely is the evolution (a) of hypertely in characters of general advantage, (b) of characters useless in the general struggle for existence, (c) of those deleterious in the general struggle for existence.

Intensity of selective advantage is more sharply graded by intra-sexual competition than by any other type of selection (see Huxley, 1938b). We may distinguish the following grades:

(a) fractional reproductive advantage. The maximum efficacy of the character is limited by the reproductive capacity of a single female; and the less successful males fall short of this by some fraction (*e.g.*, owing to inefficiency of copulatory organs or of stimulating display).

(b) All-or-nothing mating advantage: some fail to secure mates at all:

(1) Unitary mating advantage. The successful males only obtain one mate, so that the limit of advantage is again set by the reproductive capacity of a single female. This is found in monogamous species (in the broad sense). Hypertely and characters useless to the species may be generated by this.

(2) Multiple mating advantage. The successful males may obtain several mates. The limit of advantage is here set by the maximum number of mates obtained. In addition, the intensity of selection is increased, owing to the greater number of males failing to obtain a mate (polygamous and promiscuous forms). Only with this level of selective intensity do characters appear which seem to be deleterious in the general struggle for existence, as well as those which are hypertelic.

Fisher (1930, p. 131, *seq.*) on theoretical grounds believes that when there exists intra-sexual advantage among males, dependent on display, this and the capacity for the female to be stimulated by the display will reinforce each other, so that selection will initiate a "runaway" evolutionary process which will proceed very rapidly to the utmost possible limit, sometimes leading to characters deleterious in the general struggle for existence. Fisher clearly envisages the advantage accruing from distance-threat characters which obviate the necessity of fighting, but points out that selection would tend to reduce the capacity of rivals to be impressed by such characters, instead of increasing it, as he claims will occur in the females with regard to male display characters. Accordingly, he concludes, such characters may become striking but are not likely to become extravagant (hypertelic or deleterious), as with display-characters.

Darwin, to avoid the difficulty caused by the equality of numbers in the two sexes, postulated that the most efficient display would (a) be correlated with greater general vigor, (b) promote earlier mating and breeding, both of which would be of general advantage to the species. Fisher points out that, with the high rate of mortality obtaining in most wild species, early mating might confer a definite advantage. Doubtless there is some correlation between effective display and vigor, and in the human

species one sees sexual preference for certain characters connoting health (although these are often simulated by make-up). However, though this may be contributory, it cannot be the main agency promoting the evolution of elaborate epigamic characters.

Terminology. The characters considered by Darwin as indicating the existence of sexual selection fall under three heads: (a) Weapons, subserving actual combat between rivals of the same sex and species; (b) threat-characters, directed against rivals of the same sex and species; (c) characters subserving display, towards potential mates.

Weapons form part of the general category of characters concerned with combat in general, while threat and display characters form a section of the general category of allesthetic characters, effective via the distance receptors of other individuals.

The term *sexual selection* as used by Darwin should be replaced by two terms—*epigamic selection* and *intra-sexual selection.* The latter will apply to all selection involving competition between individuals of one sex in the struggle for reproduction, while the former will include selection involving display-characters common to both sexes. In cases of intra-sexual selection (and intra-specific selection in general) we must distinguish between the *component of general advantage* and the *component of (purely) individual advantage:* The ratio of these two, as indicated above, may vary within wide limits.

LITERATURE CITED

No attempt has been made to secure completeness. Many references to works on spiders are to be found in Bristowe (1929); to insects in Richards (1927); and to birds (and other organisms) in Huxley (1915, 1923, 1938).

Allen, A. A.
1934. *Auk,* 51: 180.

Beebe, W.
1931. "Pheasants, their Lives and Homes." New York.

Bristowe, W. S.
1929. *Proc. Zool. Soc.,* 309.

Darling, F. Fraser
1938. "Bird Flocks and the Breeding Cycle." Cambridge.

Darwin, C.
1871. "The Descent of Man and Selection in relation to Sex." London.

Evans, L. T.
1936. *Jour. Genet. Psychol.*, 49: 49.
Finkler, W.
1923. *Proc. Roy. Soc.* (B), 95: 356.
Fisher, R. A.
1930. "The Genetical Basis of Natural Selection." Oxford.
Haldane, J. B. S.
1932. "The Causes of Evolution." London.
Harper, E. H.
1904. *Am. Jour. Anat.*, 3: 349.
Hartley, P. H. T.
1937. *Brit. Birds*, 30: 266.
Heinroth, O.
1938. *J. f. Ornith.*, 86: 1.
Hingston, R. W. G.
1933. "The Meaning of Animal Colour and Adornment." London.
Howard, E.
1907–1914. "The British Warblers." London.
1920. "Territory in Bird Life." London.
1929. "Bird Behaviour." Cambridge.
1935. "The Nature of a Bird's World." Cambridge.
Huxley, J. S.
1914. *Proc. Zool. Soc.*, 491.
1923. *Jour. Linn. Soc.* (Zool.), 35: 253.
1932. *Nature*, 129: 166.
1938a. *Proc. 8th Internat. Ornith. Cong.* (1934), 430.
1938b. The Theory of Sexual Selection in the light of recent progress in Biology. In "Essays presented to Professor Goodrich." Oxford.
Huxley, J. S. and E. Howard
1934. *Nature*, 133: 688.
Huxley, J. S. and F. A. Montague
1925. *Ibis*, 868.
Jourdain, F. C. R.
1936. *Ool. Rec.*, 16: 25, 62.
Keith, D. B.
1927. *Brit. Birds*, 31: 66.
1938. *Proc. Zool. Soc.* (A), 108, 185.
Kramer, G.
1937. *Zts. Morph. Oekol. d. Tiere*, 32: 752.
Lack, D.
1933. *Proc. Zool. Soc.*, 23.
1935. *Ibis*, 817.
1937. *Brit. Birds.*
1938. *Proc. Zool. Soc.* (A), 108, in press.
Lorenz, K.
1935. *J. f. Ornith.* 83: 157, 389.
Marshall, F. H. A.
1936. *Phil. Trans. Roy. Soc.* (B), 226: 423.

Martin, T.
1935. (Cited from Marshall, 1936). *Trans. Dynam. Develpt.*, Moscow, 10: 181.
Meisenheimer, J.
1921. "Geschlecht und Geschlechter." Jena.
Molony, H. J. C.
1937. "Evolution out of Doors." London.
Nicholson, E. M.
1927. "How Birds Live." London.
Noble, G. K.
1929. *Am. Mus. Novit.*, No. 362.
1936. *Auk*, 53, 269.
Noble, G. K. and H. T. Bradley
1933. *Ann. N. Y. Acad. Sci.*, 35: 25.
Noble, G. K. and W. Vogt
1935. *Auk*, 52: 278.
Noble, G. K., M. Wurm and A. Schmidt
1938. *Auk*, 55, 7.
Patterson, J. T.
1928. *Biol. Bull.*, 54: 196.
Poulton, E. B.
1890. "The Colours of Animals," etc. London.
Pycraft, W. P.
1913. "The Courtship of Animals." London.
Richards, O. W.
1927. *Biol. Rev.*, 2: 298.
Roeder, K. D.
1935. *Biol. Bull.*, 69: 203.
Ryves, B. H. and Mrs. Ryves
1934. *Brit. Birds*, 28: 2, 154.
Saunders, A. A.
1937. *Auk*, 54: 202.
Scott, H.
1931. *Entom. Monthly Mag.*, 67: 241.
Southern, H. N.
1938a. *Brit. Birds*, 31: 314.
1938b. *Proc. Zool. Soc.* (A), 108, 423.
Steinbacher, G.
1938. *Beitr. Fortpfl:biol. Vögel*, 14: 55.
Sturtevant, A. H.
1915. *Jour. Animal Behavior*, 5: 351.
Verwey, J.
1930. *Zool. Jahrb.* (Allg. Physiol.), 48: 1.
Whitman, C. O.
1919. "The Behavior of Pigeons." (Posthumous Works). Carnegie Inst. Washington.
Winterbottom, J. M.
1929a. *Proc. Zool. Soc.*, 189.
1929b. *Jour. Genetics*, 21: 367.
Zuckerman, S.
1932. "The Social Life of Monkeys and Apes." London.

ORIGIN OF ATTACHED-X CHROMOSOMES IN DROSOPHILA MELANOGASTER AND THE OCCURRENCE OF NON-DISJUNCTION OF X'S IN THE MALE

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Seven occurrences of attached-X females of *Drosophila melanogaster* have been reported. Four of the females arose from sperm carrying two X's attached to each other. Two of these were related and these with the other two furnish at least three isolated examples of attachment of X's from males.

The original fly of line number 1 (following Sturtevant's (1931) numbering) was a female mosaic (found on February 12, 1921) which had developed from an X-egg (marked by mutant characters forked and Bar) fertilized by attached-X sperm of a yellow male (L. V. Morgan, 1922). The female was a mosaic having a 3X Bar anterior region and a 2X yellow posterior region. The abdomen was yellow and the fly bred as an attached-X yellow female ($\underline{y}$; underlining of symbols denotes attachment of designated chromosomes).

Lines number 3 and 4, established by Dr. Sturtevant, arose from two males that appeared in consecutive generations. Details of the pedigree (Sturtevant, 1931) are of interest in connection with the most probable explanation to be offered. Among the offspring of a B/f B fu female backcrossed to a forked Bar fused male one wild-type male was found (July 23, 1923, perhaps by contamination). The wild-type male was mated to an attached-X yellow female and among its off-spring were two flies that are to be noted. One was an attached-X wild type female (original female of line 3). The other was a wild type male which, like its father, when mated to an attached-X yellow female produced an attached-X wild-type daughter (original female of line 4). Clearly the wild-type females had received attached X's from their fathers which were related to each other as father and son.

A line which may be called number 5 arose similarly from attached-X sperm in a culture of Bar bobbed males mated to attached-X yellow females. The original female, found on December 30, 1929, by Dr. Curt Stern (U), was an attached-X B bb female (not showing bb because of the presence of a Y chromosome).

Another line (number 6) of attached-X's has been distributed from Moscow and was found prior to November, 1932. The line, homozygous for scute apricot, is used in the laboratory in Pasadena, but references to its origin are not available and it will not be included in the discussion.

Two other attached-X females have been found; the X's, however, have been identified as received from the mothers. Line number 2 (Anderson, 1925) arose from the attachment of the two X-chromosomes of a female which had been x-rayed soon after hatching. One chromosome (a crossover in a distal region) was proximally attached to an unlike non-crossover chromosome. The x-rayed female had carried genes for scute apricot crossveinless tan forked in one chromosome and genes for broad echinus cut^6 garnet in the other, and she had been mated to a Bar male. The attached-X daughter was homozygous for broad and echinus, and in some of her progeny the more proximal mutant characters became homozygous by crossing-over showing that her constitution had been $\underline{br\ ec\ cv\ t\ f/br\ ec\ ct^6\ g}/Y$.

More recently (L. V. Morgan, December 29, 1936) another attached-X line (number 7) has been found in which the two different X's also came from a female. The steps by which this came about can be followed in the pedigree. In order to show the sequence of the events it is necessary to go back to a line of attached-X yellow females mated to multiple mutant males called "7ple" which is not yellow. On September 24, 1924, besides the regular yellow females, a wild-type detached-X female was found, due to crossing-over between Y and an X in the female parent (Fig. 1, a_1). Kaufmann (1933) has shown that such females receive from their mothers a chromosome composed of an X and

one arm, short or long, of a Y chromosome ($\underline{XY}^{S \text{ or } L}$) which are carried by the spindle fiber attachment originally belonging to the Y (Fig. 1, b_1); the other arm of the Y has been replaced (by crossing-over) by the X. The not-yellow female was bred and her offspring were those to be expected from a detached-X female carrying a lethal mutant and suppressor of crossing-over in the yellow chromosome that had been received from the mother, and a "7ple" (not-yellow) chromosome from the father. In subsequent generations males carrying the yellow semilethal chromosome ($\underline{XY}^{S \text{ or } L}$) were infrequent, sterile and usually showed somatic disturbances such as serrated wing margins. Backcrosses were made to yellow garnet^2 forked bobbed^1 (lethal) males and for many generations two lines a and b were carried on by selection of virgin yellow females, heterozygous for the y l chromosome (attached to an arm of Y), mated to y g^2 f bb^1 males taken from a stock that was carried on against attached-X or ClB.

To obviate the need of selection, yellow females of line b and, in another bottle, 3 yellow females of line a were mated to wild type InAM males on December 12, 1936. On December 29, when the cultures were examined, it was found that whereas line b gave the expected classes of offspring (wild-type females and y g^2 f bb^1 males) the offspring of line a were all yellow females and wild type (InAM) males except one yellow forked female and two wild-type females. The count was typical for a yellow female carrying attached X's homozygous for y and heterozygous for f. In the next generation the yellow females backcrossed to InAM males continued to give matroclinous females and patroclinous males and the usual exceptions from attached-X females. In detail, a mass culture of F_1 yellow females mated to wild-type InAM brothers gave, in F_2, 52 yellow females, 1 crossover $\underline{y\ f}$ female, 1 wild-type $\underline{XXX}$ female, 100 wild-type males, 1 y f male. (In later counts the ratio of $\underline{y}$ females to wild-type males was nearer to 1 : 1).

The $\underline{y\ f}$ attached-X female mated to brothers gave 37 $\underline{y\ f}$ females, 31 wild-type males and 1 y f male, showing that

her chromosomes had been attached. Garnet[2] had apparently been lost in the ancestry of the attached-X individuals that were mated. The two F_2 wild-type females were of the infrequent kind of female that carries a single chromosome from her mother derived from X/Y crossing-over. They gave regular classes in the expected ratios. One had received a y g^2 f (bb^1 ?) chromosome attached to an arm of Y and her offspring were: 90 wild-type females, 30 y g^2 f males, 43 wild-type males, 2 y males and 1 g^2 f male. (InAM nearly suppresses crossing-over.) The other F_2 wild-type female had received a y f chromosome from her mother and her offspring were: 67 wild-type females, 24 y f males, 32 wild-type males and no cross-overs. A line from the F_1 attached-X yellow females is referred to as number 7.

The lines described show two origins of attached-X's, namely, attachment of sister X-chromatids in males and attachment of two different X-chromosomes in females. At first sight there seem to be two different problems, but they may in fact be resolved into one.

Two X-chromosomes could become attached if there were a chromosome having two arms either of which could be replaced by an X-chromosome. Such a chromosome is the Y, both of whose arms are in part homologous to X (Kaufmann, 1933, Neuhaus, 1936). The formation of attached-X's might take place by two steps, first, the replacement of one arm of Y by an X, and subsequently the replacement of the other arm by another X or by a second strand of the same X. It can be shown that two such steps, in fact, occurred in the formation of line 7 by tracing the history of the y l component of its attached-X's.

Since the y l chromosome arose from crossing-over in an $\underline{XX}Y$ female between an X and an arm of Y (Fig. 1, a_1), the X and the other arm of the Y were carried by the spindle fiber attachment that had belonged originally to the Y (Fig. 1, b_1). During the period when the stock was carried on by selection of yellow females (supposedly carrying a y l X-chromosome attached to an arm of Y ($\underline{XY}^{S\text{ or }L}$) and a separate y g^2 f bb^1 X) crossing-over

probably took place between the arm of Y, attached to the y l X-chromosome, and the y g^2 f bb^1 X-chromosome (Fig. 1, c_1). The exchange might have occurred at the 4-strand stage (6-strand for the region homologous to the Y component) or in a previous cell generation. The attached-X females developing from gametes that received the attached-X's thus formed ($\underline{y^1/y\ g^2\ f\ bb^1}$♀, Fig. 1, d_1) were yellow but produced no y males. Since yellow males had

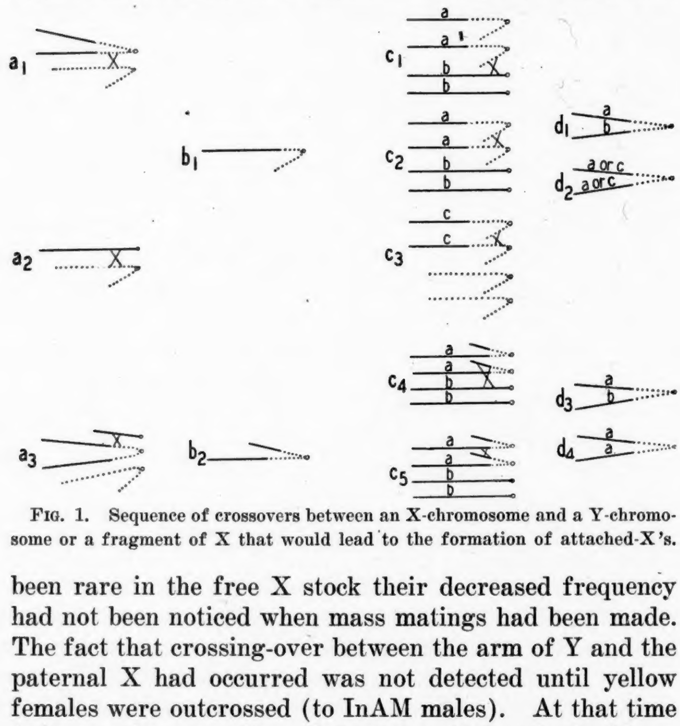

FIG. 1. Sequence of crossovers between an X-chromosome and a Y-chromosome or a fragment of X that would lead to the formation of attached-X's.

been rare in the free X stock their decreased frequency had not been noticed when mass matings had been made. The fact that crossing-over between the arm of Y and the paternal X had occurred was not detected until yellow females were outcrossed (to InAM males). At that time (after random sampling of about 6 to 10 females had been made for an unknown number of generations) the attached-X females had so far replaced those carrying free X's that the three females mated to InAM males had all carried attached-X's.

The new attached-X line had originated by two steps first crossing-over between attached-X and an arm of Y,

second crossing-over between the other arm of Y (attached to X) and another X.

It may be assumed that attached-X females that have received their X's from sperm may have a similar origin. The first step, crossing over between X and Y may occur in $\underline{XX}Y$ or in XXY females, but the most frequent source of an $\underline{XY}^{\text{s or L}}$-chromosome is crossing over in the male (Stern, 1929, Neuhaus, 1946a and b, 1937) since this may occur in any line (Fig. 1, a_2). An $\underline{XY}^{\text{s or L}}$-chromosome may be transmitted from female to female or may be transmitted back and forth from male to female in the usual manner of criss-cross inheritance of X. If the second step, namely, crossing-over between the arm of Y and the X-chromatid not attached to it, occurs in a male (at the 4-strand stage of spermatogensis, Fig. 1, c_3) the chromosomes of sperm carrying attached-X's (Fig. 1, d_2) may be recovered provided the male gamete makes a viable combination with an egg gamete. It will very rarely be recovered in ordinary stocks in which it can usually form only an inviable $X\underline{XX}$ zygote. The most frequent gametes (in the laboratory) that are suitable are the Y-eggs of attached-X females, and it is from these that all but one of the lines from attached-X sperm arose.

The origin of line 1 from elimination of a chromosome in an $X\underline{XX}$ female in such a way that the life of the fly was saved and that the fly was fertile as an attached-X female is scarcely to be expected at all.

Neuhaus (1937) used attached-X females mated to $\underline{XY}^{\text{s or L}}$ males to measure the frequency of crossing-over between the arms of Y and X by the frequency of patroclinous attached-females among the offspring.

Lines 3 and 4 from attached-X sperm can be explained if the original not-B chromosome had carried an arm of Y from previous X/Y crossing-over. In the male that received the not-B chromosome and was mated to an attached-X yellow female it may be inferred that the second crossover step took place, and that attached-X sperm fertilized a Y-egg and produced an attached-X wild-type female. If the explanation is correct, the not-B male

transmitted the $\underline{XY}^{S \text{ or } L}$-chromosome to his sons. In one son the second crossover step likewise took place, and mated to an attached-X female he also produced an attached-X wild-type female. The explanation is the more probable in that the transmission of the $\underline{XY}^{S \text{ or } L}$-chromosome from father to son affords the opportunity for formation of attached-X females in two successive generations.

It follows from the analysis that the X's of attached-X females, if derived from the succession of the two crossover steps that have been described, are carried by the spindle fiber attachment that originally belonged to a Y-chromosome. The attachment of two X-chromosomes is made possible by the position of the spindle fiber attachment in the Y and the homology between both arms of Y and X.

A cycle from attached-X to attached-X, similar to that which had occurred in line 7, occurs in lines that carry a duplicating fragment of the X-chromosome (Philip, 1934; Stern, 1937; Morgan, 1938). The first required crossing-over takes place between the fragment (instead of Y) and X in a female of constitution $\underline{XXX}^{Dp}Y$ (Fig. 1, a_3). By this exchange an X with a fragment attached to it is formed ($\underline{XX}^{Dp}$, Fig. 1, b_2).

An egg containing the new kind of chromosome (Fig. 1, b_2) fertilized by X-sperm produces a female heterozygous for the $\underline{XX}^{Dp}$ chromosome. When crossing-over in such a female takes place between the fragment and the free X (Fig. 1, c_4) two different X's become attached to each other (Fig. 1, d_3). Attached-X females carrying two different maternal X's have been recovered from duplication females whose X's were suitably marked (Morgan, 1938). Crossing-over also occurs (half as frequently) between the fragment and the sister X-chromatid to which the fragment involved in crossing-over is not attached (Fig. 1, c_5). This must occur at the 4- (partially 6-) strand stage. Homozygous attached-X females thus produced have also been found (cf. Fig. 1, d_4).

An event parallel to the last but involving Y instead of

TABLE I

PATROCLINOUS FEMALES, THEIR PARENTAGE AND OFFSPRING. LINES 1, 3, 4, 5 IN WHICH THE X'S WERE ATTACHED ARE NOT INCLUDED

No.	Date	P_1	F_1 patroclinous female	X characters of mate	F_2 ♀♀		♂♂	
1	3.4.21	w^e ct f/f B ♀ x y ♂	mosaic het. B y XXX XX	w^e ct^6 v f	f	not–f		y
2	2.21.21	w^e ct f/f B ♀ x y ♂	mosaic not–y y XXX XX					
						F_2 wild-type ♀ × y ♂		
3	1922	w^e ct f/f B ♀ x y ♂	y	not–y	F_3 y	+	y	not–y
						F_2		
4	Gershenson (1929)	y/y/Y ♀ × w sml f B ♂	w sml f B	+	B 120	w sml f B 1	w sml f B 29	+ 3
5	1923	y/y/Y ♀ × f B ♂	f B	w^a	het. B 72	f B 1	f B n	w^a 1
6	1923	y/y/Y ♀ × w^a ♂	w^a	f B	het. B 208	w^a 1	w^a n	f B 1
7	1923	y/y/Y ♀ × w^a ♂	w^a not virgin?	f B	het. B 21 + n	w^a 28 + n	w^a 24 + n	f B 0
8	1923	y/y/Y ♀ × w^a ♂	w^a (died)	f B				
9	1923	y/y/Y ♀ × w^a ♂	w^a	w^a	w^a			
						F_3		
					w^a		w^a	
						F_2		
10	1923	y/y/Y ♀ × w^a ♂	w^a	w^e m	w^{e-a} 34	w^a? 4	w^a 23	
11–18	1923	y/y/Y ♀♀ × w^a ♂♂	w^a					
19	1924	y/+/Y ♀ × w^e g B ♂	w^e g B	m	het. B 23		w^e g B 33	m 1
20	1924	y cv v/v B/Y ♀ × f B ♂	f B not virgin?	w^e m	f B 8	het. B 1	f B 4	
21	1924	sc ec cv v g f/y/Y ♀ × f B ♂	f B (died)					
22	1937	Dp–100/y w cv v f/y^2/Y ♀ × y^2 cv v B ♂	y^2 cv v B	f fu	het. B 55		y^2 cv v B 53	y^2 cv v 1, f fu 2
23	1937	Dp–100/y w cv v f/y^2/Y ♀ × y^2 cv v B ♂	y^2 cv v B					
24	1927	Dp–100/y/y/Y ♀ x y w f B ♂	w f B XXXDp (Y?)	y cv lz	het. B 31	y het. B 42	y w f B 31	
25	1923	Dp–100/y/y/Y ♀ × f B ♂	f B	v	het. B 88	f B 22	f B 87	v* 48
26	1923	Dp–100/y/y/Y ♀ × f B ♂	f B	v	het. B 75	f B 27	f B 83	v* 0

* Records of F_2 f B ♀♀ mated to w^a ct v f ♂♂ are similar to those for F_1.

an X fragment would be crossing-over at the 4- (partially 6-) strand stage in an $X\underline{XY}^{S \text{ or } L}$ female between the arm of Y and the sister chromatid of the X-chromatid to which the Y is attached (diagonal crossing-over, Fig. 1, c_2). An $\underline{XX}Y$ female containing the attached-X's would not be distinguishable from one that had originated from equational non-disjunction, unless tested for attachment of X's (Fig. 1, d_2).

A reciprocal crossover between $Y^{S \text{ or } L}$ or X^{Dp} and the strand attached to it would not form attached X's.

The origin of attached-X females from crossing-over in $\underline{XY}^{S \text{ or } L}$ males (Neuhaus) or in $X\underline{XY}^{S \text{ or } L}$ females (as evidently occurred in line 7) does not exclude the possibility that they may originate also from incomplete division of X in the male.

It has been shown by Gershenson that non-disjunction of two separate X's may occur in the male. His complete description shows clearly that a patroclinous daughter of an attached-X yellow female was an XXY female that had received two separate X's from her father and a Y from her mother (Table 1, No. 4).

There are similar complete records of seven other patroclinous females, and records of four more (Table 1, Nos. 3, 7, 9 and 20) show at least that two separate X's had been transmitted through sperm.

One, probably two of these females (Table 1, Nos. 1 and 3) started as XXX females and, after elimination, at an early stage of development, of one X, bred as females that had received two separate X's from their fathers. Their parents were of the same stocks as those of the mosaic whose X's were attached and from which line 1 of attached-X's originated. The three mosaics were found during a short period of high frequency of occurrence of gynandromorphs and mosaics.

The remaining nine patroclinous females of which there are records were found while studying the original line of attached-X and others derived therefrom, namely, a line of attached-X triploids and various lines of Duplication-100,

and among offspring of attached-X females counted by Miss E. M. Wallace.

Seven had developed from Y-eggs of attached-X females to which the males that produced the non-disjunctional sperm had been mated.

One female (Table 1, No. 22) developed from a Y-egg of a female ($XXX^{Dp}Y$) that carried a free X, an X with a fragment of $\overline{X}$ (Dp-100) attached to it and a Y. Such females produce 9 per cent. Y-eggs (Morgan, 1938).

One female (Table 1, No. 24) developed from an egg containing a fragment (Dp.-100). Her mother ($\underline{XX}X^{Dp}Y$) carried attached-X's (homozygous for yellow) a fragment of X and a Y (a sex chromosome complement giving about 12 per cent. eggs carrying a fragment with or without a Y, and no X-chromosome; Morgan, *loc. cit.*). The egg had been fertilized by sperm containing two separate X's and the zygote was a female patroclinous in the sense that she showed the recessive characters of her father, for which there were no normal allelomorphs in the duplicating fragment. In her non-duplication sons the other recessive paternal characters also showed.

Twelve additional females from the same sources have been recorded as showing recessive characters of their fathers unlike those of their mothers (Table 1). As there are no records of breeding it is not known whether or not the X's were separate.

Two experiments provide data that may have a bearing on the frequency of non-disjunctional sperm. In one experiment Miss Wallace counted 4,257 regular apricot (w^a) males from Y-eggs of attached-X yellow females fertilized by X sperm of w^a males and 9 patroclinous w^a females from Y-eggs fertilized by 2X-sperm. Unfortunately there is a record of only one mated w^a female (Table 1, No. 10); it shows that she had received separate X's from her father.

A y^2 cv v B female (Table 1, No. 22) was one of two patroclinous daughters (one not tested) of females carrying an X marked by y w cv v f to which the fragment of Dp-100 was attached, a separate X marked by y^2 and a Y (Morgan, 1938). The tested female had developed from

a Y-egg fertilized by non-disjunctional separate X sperm.

In both of these experiments there was 0.2 per cent. of sperm carrying two X's. There is no criterion by which to determine whether all these were separate X's. But judging from available data it is probable that a large proportion were not attached. It appears that 2X sperm occurs more frequently from non-disjunction of separate X's than from formation of attached-X's, for among fifteen tested cases of 2X sperm (lines 3 and 4 of attached X's are referable to one original X/Y crossing over) twelve proved to be separate X's. Furthermore, the possible origin of attached X's from incomplete separation would seem to be, if occurring at all, the most infrequent; there are only two cases without evidence opposed to that interpretation, for among the six known cases of attached-X's the two from females (lines 2 and 7) are excluded, and for lines 3 and 4 the evidence has been shown to be in favor of the other explanation that is X/Y crossing-over.

Two patroclinous females of a different kind developed from Y-eggs of duplication females carrying attached-X's ($\underline{XX}X^{Dp}Y$) mated to males taken from f B stock at about the same time (Nos. 25 and 26, Table 1). Each produced one patroclinous daughter, which was mated to a vermilion male. Both patroclinous females gave high non-disjunction, one of them certainly in two generations (the second generation mated to w^a ct v f males). The other patroclinous female gave a high frequency of exceptional females, but no exceptional males in the first generation, and fewer exceptional females and again no exceptional males in the second generation mated to w^a ct v f males. The absence of the exceptional males is not explained. Otherwise the records indicate that the two males from f B stock carried a translocation for the X-chromosome, since their daughters and again their daughters gave high non-disjunction.

Summary

Two X-chromosomes of *Drosophila melanogaster* may become attached to each other by replacement of the two arms of a Y by X's. The first step, crossing-over between

one arm of Y and X, is known to take place in $\underline{XX}Y$ females and in males (XY) (Kaufmann, Neuhaus), and may take place in XXY females, forming an $\underline{XY}^{\text{S or L}}$ -chromosome. The second step, crossing-over between an arm of Y attached to X and another X, has been observed in males (Stern, Philip, Neuhaus).

An $\underline{XY}^{\text{S or L}}$ -chromosome may be transmitted in the same way as an X, back and forth from males to females or directly through females in stocks with separate X's, or directly through males in attached-X stocks.

The second step is known to take place in males in the 4-strand stage of spermatogenesis, two like X's becoming attached to each other. The chances of recovering the attached X's will depend upon the frequency of egg nuclei with which the $\underline{XX}$ sperm may produce a viable zygote.

If the second step takes place in a heterozygous female of $X\underline{XY}^{\text{S or L}}$ constitution, between the arm of Y and the chromosome unlike the one to which the arm is attached, two unlike X's will become attached to each other.

The two steps have been followed in the history of line 7 of attached-X which shows that the first step occurred in an $\underline{XX}Y$ female and the second step in an $X\underline{XY}^{\text{S or L}}$ female.

Anderson recovered different maternal X's attached together from an x-rayed female.

Four females received attached-X's from their fathers. The origin of attachment of the X's may have been two steps of X/Y crossing-over (as was found in line 7) or it may have occurred from incomplete separation of X's in a male. Relationship of two of the four females makes the first explanation the more probable for these two.

Non-disjunction of two completely separated X's in the male has been found by Gershenson and has been observed in eleven other instances. Nearly all were recovered from Y-eggs of XXY females, one from a Y-egg of an $\underline{XX}X^{\text{Dp}}Y$ female and one from an egg that had received the duplicating fragment of an $\underline{XX}X^{\text{Dp}}Y$ female.

Twelve patroclinous females from the stocks that gave those having separate X's from their fathers have not been tested for separate X's.

There is evidence from two experiments that about 0.2 per cent. of sperm carried two X's. It is not proved that the X's were not attached, but among fourteen scattered and unprejudiced instances of 2X sperm (from these two and other experiments) only two showed attachment of X's.

In brief, tested cases of inheritance of two X's from one parent are: twelve females that received separate X's from the male; one female (of line 7) having attached X's from the female whose history shows the origin to have been by two steps of crossing-over between X and Y; two females (of lines 3 and 4) whose relation to each other points to their origin by two steps of crossing-over between X and Y; two isolated instances of females that received attached-X's from their fathers; two females that received two paternal X's, one X being involved in a translocation.

LITERATURE CITED

Anderson, E. G.
1925. *Genetics*, 10: 403–417.
Gershenson, S.
1929. *Biol. Zentr.*, 49: 509–510.
Kaufmann, Berwind P.
1933. *Proc. Nat. Acad. Sci.*, 19: 830–838.
Morgan, L. V.
1922. *Biol. Bull.*, 42: 267–274.
1924. *Genetics*, 10: 148–178.
1938. *Genetics* (in press).
Neuhaus, M. J.
1936a. *Z. i. A. V.*, 71: 265–175.
1936b. *Nature*, 137: 996.
1937. *Genetics*, 22: 333–339.
Philip, Ursula
1934a. *Z. i. A. V.*, 67: 446–476.
1934b. *Nature*, 133: 726.
1935. *Jour. Genetics*, 31: 341–352.
Stern, Curt
1926. *Biol. Zentr.*, 46: 505–508.
1929. *Z. i. A. V.*, 51: 17–353.
1936. *Genetics*, 21: 625–730.
Stern, Curt, and Dorothy Doan
1936. *Genetics*, 21: 625–730.
Sturtevant, A. H.
1931. *Pub. Carnegie Inst. Wash.*, 421: 63–81.

THE INTERRELATIONS OF INVERSIONS, HETEROSIS AND RECOMBINATION

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There is a rapidly growing body of evidence to show that wild strains of many organisms are heterogeneous for inverted sections of the chromosomes. The occurrence of specimens heterozygous for inversions, in one or more chromosomes, has now been recorded in so many species of plants and of insects that there can be little doubt that they are to be expected in almost any large sample, at least of organisms not normally propagating by self-fertilization.

Certain consequences of inversions, as concerned with the behavior of mixed populations, have not yet been adequately discussed. In particular, it was briefly mentioned by Dobzhansky and Sturtevant (1938—p. 61) that "heterozygosis for inversions decreases the amount of crossing over, and this may be of selective value in connection with heterosis effects." The present paper is a more detailed consideration of this question.

In individuals heterozygous for an inversion no effective crossing over occurs unless the inversion is, genetically speaking, a very long one. The single cross-over chromatids are unbalanced and in fact eliminated (Sturtevant and Beadle, 1936); effective recombination results only from two-strand or three-strand double crossing over. This is, of course, rare in any but long inversions. It has also been shown that, as a result of the elimination of the cross-over chromatids, the fertility of a female heterozygous for an inversion is not reduced, unless complementary, or four-strand, double crossing over occurs. Again this will be rare unless the inversion is long (Sturtevant and Beadle, *loc. cit.*). The loss of fertility from such double crossing over is obviously completely correlated with the effective recombination.

Thus, if a chromosome exists, in a population, in two sequences, differing by an inversion, it will in effect show two distinct lines of descent. There is free exchange of material within any line (*i.e.,* sequence), but none between the sequences. Therefore, fluctuations of the genic contents must occur almost independently in the two sequences. Under such conditions it is inevitable that in time the gene content of the two sequences will become different. It must be supposed that each sequence is susceptible to the same mutations, and with the same frequencies, but, as a result of the relative rarity in a population of a given mutant allelomorph at any one moment, certain genes will be present in one sequence and not in the other. Elimination of mutant genes, both by chance and by selection, will insure that the gene contents of the sequences are unlike. The gene content of any sequence must be always fluctuating, and over a great length of time must, on the average, be the same as that of any other sequence. The point which we wish to make is, however, that at any given moment, for any given population, the gene contents of the two (or more) sequences will be unlike, and each will carry mutant allelomorphs that are lacking in the other types.

It is thus clear, considering two sequences A and B, that the homozygotes AA and BB are more likely to be homozygous for deleterious recessive mutations than is the sequence heterozygote AB. It may be noted here that we need only consider deleterious recessives, as these are presumably by far the most common type of mutation in wild populations, as well as in laboratory stocks. Then in general the sequence heterozygote AB will be at a selective advantage with respect to either of the corresponding homozygotes.

It does not seem desirable to give a detailed algebraic analysis of this question, because, as pointed out above, there can be no stability in the exact relations of the sequences with each other. A few results are, however, of some importance.

In the first place a single gene difference can not in general cause such heterosis. The simplest effective condition is that in which each sequence contains a deleterious recessive not present in the other. Two recessives existing in the two sequences with unlike frequencies may cause heterosis, but this will lead to leveling of the frequencies of occurrence of the mutant genes in the two sequences, and so such heterosis will not be persistent. Secondly, if sequence A exists with frequency p, and B with frequency $q (q = 1 - p)$, in a population; and if, letting the fertility of type AB be 1, AA has fertility $(1 - a)$ and BB $(1 - b)$,

$$\frac{p}{q} = \frac{b}{a} \quad \text{or} \quad pa = qb = k$$

for the point of equilibrium. With more than two sequences the question is complicated by the inequality of the various heterozygotes in fertility. It is, however, clear that, at equilibrium, the sequence frequencies, p, q, r, etc., will be inversely proportional to a, b, c, etc., the loss in fertility of the corresponding homozygotes. In general, on the assumption that each sequence is subject to the same mutations with the same frequencies, a must tend to equal b, etc., over any length of time. In consequence there will be a tendency for the various sequences to exist with equal frequencies in the populations. This will, of course, be subject to the effect of large local and temporary fluctuations. Equality in frequency of the sequences is the mid-point of the fluctuation range.

Thus, when an inversion arises it will at first depend largely on chance for its opportunity to become established. After it has persisted for sufficient time to differentiate relative to the other sequences present, there will be a considerable selective action favoring individuals carrying it in the heterozygous state. In consequence, its chance of total loss will be much reduced. Equally, of course, its chance of completely replacing the other sequences already present will also be very small.

We have so far considered the fate of inversions when

once established, but on turning attention to the origin of inversions it is immediately obvious that not all chromosomes in all wild populations are heterogeneous for sequence. In particular, whereas the third chromosome of *Drosophila pseudoobscura* shows a wealth of variation in this respect (Dobzhansky and Sturtevant, 1938), the X,[1] second and fourth only occasionally show heterogeneity in sequence. What is the explanation?

It would appear that this is but a specific case of a more general question, that of the advantage of crossing over, and also of recombination of non-homologous chromosomes. This has often been discussed (*e.g.*, by Muller, 1932, Darlington, 1932, p. 456, and Fisher, 1930, pp. 102–104). Two solutions have been proposed, viz.: (a) that recombination makes it possible to obtain favorable combinations of mutant types which have arisen independently, and (b) that recombination increases the "flexibility" of the species in its ability to adapt itself to ever-changing environmental conditions.

The former suggestion clearly indicates an advantageous property of recombination, but it would seem that the resulting selection in favor of crossing over would be small, since such recombination need occur but once. Indeed subsequent recombination would be disadvantageous in breaking up the new favorable combination. Further, the opposite effect of unfavorable mutations would appear to oppose and probably to outweigh this selective action favoring recombination (see discussion of a similar case where secondary effects of favorable mutations are opposite in sign to secondary effects of unfavorable ones—Sturtevant, 1937).

[1] We are not aware of any case in which there is a heterogeneity of sequences in the sex-chromosomes of a wild population, except that associated with "sex-ratio" in certain species of Drosophila (Sturtevant and Dobzhansky, 1936). This constitutes a special case, where the heterogeneity for the sex-ratio gene is maintained by a mechanism quite different from the one discussed above. In fact, the present mechanism, being dependent on unfavorable recessive mutant genes, would be expected to be much less effective on the sex-chromosomes, since such recessives are regularly rapidly eliminated in the heterozygous sex.

The second possibility, concerning the "flexibility" of the species, seems to be of greater moment, but it has never been analyzed in sufficient detail to bring out the essential prerequisites for its functioning.

The simplest system that we have been able to devise, having the required property of favoring recombination, is as follows: Two gene pairs, A,a and B,b, exist in a population subjected frequently to three different sets of environmental conditions, D,E and F. Condition D favors A but acts unfavorably on B, whereas E favors B but lowers the frequency of A. These, if properly adjusted as to intensity of selection and number of generations over which they operate, will insure the perpetuation of both allelomorphs at each locus. Recombination will not, however, be of importance. For this it seems necessary to introduce the third condition, F, favoring the combination AB (with or without a similar effect on ab), but acting adversely on the single types A and B. Under such conditions it would appear that there will be a selective action favoring recombination, of the order of magnitude of the selection of the AB type, as opposed to Ab or aB, under condition F. Other combinations of two or more loci may be exerting similar action in similar or dissimilar environmental conditions, and so the net effect will probably be to favor recombination for the majority of loci under the majority of condition changes. The crucial point of the argument is, of course, that environmental changes which must be supposed to be each decisive for the fate of one or more generations, can not decrease recombination but can favor it. This is in sharp contradistinction to the earlier suggestion, where recombination, once having occurred, is acted against.

If we agree that recombination is favorable and selected in some such way as this, we can suggest a reason for the special case of the almost complete confinement of sequence heterogeneity to one chromosome in *Drosophila pseudoobscura.* The first inversion to arise in a chromosome will, on its becoming common in the population,

severely reduce the effective recombination in that chromosome, and, of course, in the whole nucleus (its effect may be partially, although not completely, compensated by increases of recombination in other chromosomes). A second inversion in that chromosome will result in less reduction in recombination, a third in still less, and so on. On the other hand, a new inversion in a *different* chromosome must produce an effect more or less equal to that of the first sequence change, in its reduction of recombination. Consequently once one chromosome shows a sequence change, further similar changes are much more likely to become established in that same chromosome than they are in others. The first chromosome to show a change of sequence may achieve this distinction by pure chance, but subsequent events will then result in the reduction of the chance of inversion heterogeneity in other chromosomes, as these would severely reduce recombination. Any further heterogeneity that should arise in that same chromosome will, however, be maintained by the heterosis effect. The two effects, recombination reduction and heterosis, are in opposition, and their balance will determine the fate of inversions arising in a wild population. A similar diversification in the properties of chromosome sections, with respect to recombination frequencies, has been postulated by Darlington (1936) for Oenothera.

LITERATURE CITED

Darlington, C. D.
1932. "Recent Advances in Cytology," (first edition). London.
1936. *Jour. Genet.*, 32: 343–352.
Dobzhansky, T., and A. H. Sturtevant
1938. *Genetics*, 23: 28–64.
Fisher, R. A.
1930. "The Genetical Theory of Natural Selection." Oxford.
Muller, H. J.
1932. AM. NAT., 46: 118–138.
Sturtevant, A. H.
1937. *Quart. Rev. Biol.*, 12: 464–467.
Sturtevant, A. H., and G. W. Beadle
1936. *Genetics*, 21: 554–604.
Sturtevant, A. H., and T. Dobzhansky
1936. *Genetics*, 21: 473–490.

VARIATION AMONG INSULAR MAMMALS OF GEORGIA STRAIT, BRITISH COLUMBIA

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WITH material available from six of the islands in Georgia Strait, it has seemed desirable to indicate the variation among some small mammals found on them. The specimens, excepting those from Saturna Island, all were obtained by the late Mr. R. A. Cumming, of Vancouver, British Columbia. The death (Turnbull, 1937) of Mr. Cumming last July renders impossible of accomplishment the plan that he and I had for a joint account correlating the structural variations with differences, which he alone had detected, in habitats and habits of the animals concerned. These and other zoological findings were lost with our fellow naturalist.

DEERMICE (*Peromyscus*)

Of the *Peromyscus* studied, all are of the species *Peromyscus maniculatus*. The variations detected, excepting those ascribable to season, sex, age or individual variation such as may ordinarily occur in animals of the same litter, are mainly in external proportions as determined from the conventional measurements of length of body, tail and hind foot, and in size of skull and in some instances its shape. These are described in detail under headings of "Diagnosis" and "Variation of Insular Populations" beyond. Color is relatively uniform: the variations noted are more grayish sides in the northernmost (Savary Island) population, and lighter, more reddish sides in the southernmost (Saturna Island) population. Possibly, as pointed out by Engels (1936), the mainland population and that from Bowen Island average slightly darker on the sides than those from more western islands. However, as a means of distinguishing one population from another, color has been of but little use, except for the

deermice on Saturna Island, which are distinguishable from those of the other islands by lighter sides and distinct lateral line.

The question of how best to portray the variation detected has been a perplexing one. The samples in general are too small to make worthwhile the application of most of the mathematical tests and expressions of variations involving computation of the probable error. The variations were analyzed, however, by Snedecor's (1934) formula for testing the homogeneity of populations, and although the differences proved to be significant in the sense that they were not due to random sampling, the resultant expressions (numerals) of difference are hardly impressive. Nor does the plan of Engels (1936), comparing few populations, lend itself to comparison of a number of forms as large as we now have. Graphs were found cumbersome when the variation in each character was plotted.

The plan of giving a different subspecific or specific name to the population of each island has much in its favor. However, there is some overlapping of characters between some populations of islands near one another, so that a few individuals can not certainly be identified. Moreover, if mice, different on each island, should become available from, say, 30 of the islands in the Strait, the formal naming of each might not be the best method of cataloguing the variation. For these reasons the system of naming every insular population was discarded.

Finally, the following plan was adopted: (1) Four formal subspecific names are employed, one for the mainland animals, one for those on Vancouver Island, one for those on Saturna Island and one (here newly proposed) for the mice on all the five more northern islands. (2) Texada Island is chosen as the type locality for the subspecies on the northern islands, and the population there is taken as one established point of reference and employed in making comparisons of the other insular populations. (3) In the diagnoses and comparisons, the kinds of variation

found are mentioned. (4) In the table of mean measurements the amount, or degree, of variation is indicated, as it is also in Fig. 2 for length of tail.

Systematically, this "lumping" of the several insular populations under one name has in its favor the possession by all 5 stocks of a short tail, large skull, similar (though not diagnostic) coloration and in all but one (Lasqueti Island) a long body. The new subspecies may be known as:

Peromyscus maniculatus georgiensis new subspecies

Georgia Strait Deer Mouse

Type. Female, subadult (M^1 with tubercles one-third worn down), skin and skull; no. 70400, Mus. Vert. Zool.; Vanada, Texada Island, Georgia Strait, British Columbia; May 4, 1936; collected by R. A. Cumming; original no. 1518.

Range. Known from Savary, Texada, Lasqueti, Thormanby and Bowen Islands in Georgia Strait, British Columbia.

Diagnosis. Body large; tail short; hind foot long; skull in general long and narrow, especially long in nasals, diastema, and shelf of bony palate, but broad across mastoidal region.

Comparisons. Topotypes compared with *P. m. austerus* from Vancouver on the mainland uniformly have shorter tails, longer bodies and, on the average, longer hind feet, and skulls larger in all recorded measurements except interorbital breadth, length of diastema and length of anterior palatine foramina, which measurements are about equal in the two races.

Compared with *P. m. angustus* from Alberni Valley, *georgiensis* is similarly distinct as regards short tail and long body, and in every cranial measurement it averages larger. The difference in cranial dimensions is more, and in length of tail less, than between *austerus* and *georgiensis*.

Compared with *P. m. saturatus, georgiensis* is distinguished by longer tail relative to body, longer hind foot, grayer sides, absence of lateral line and a skull that averages larger in all measurements taken except the length of the tooth row which is about the same as, or greater than, in *saturatus*.

TABLE 1

AVERAGE MEASUREMENTS, IN MILLIMETERS, OF POPULATIONS OF PEROMYSCUS MANICULATUS FROM SOUTHWESTERN BRITISH COLUMBIA

Locality	Number of specimens of each sex	Total length	Length of tail	Length of hind foot	Greatest length of skull	Basilar length	Zygomatic breadth	Interorbital constriction	Length of nasals	Shelf of bony palate	Incisive foramina	Diastema	Postpalatal length	Maxillary tooth-row	Mastoidal breadth
Savary Island	10 ♂	171	82	22.3	27.1	20.6	13.4	4.0	11.2	4.0	5.5	7.3	9.6	3.9	11.3
	4 ♀	172	82	22.1	26.1	19.6	13.2	4.1	10.7	3.7	5.4	7.1	9.3	3.8	11.1
Texada Island															
Vanada	5 ♂	165	68	22.3	26.8	20.7	13.9	4.0	11.3	4.0	5.7	7.5	9.9	3.9	11.6
	6 ♀	170	69	22.9	27.0	20.6	13.6	4.0	11.4	4.1	5.5	7.3	9.7	3.9	11.0
Anderson's Cove ..	7 ♂	169	71	22.1	26.8	20.4	14.0	4.1	11.3	4.1	5.6	7.3	9.5	3.9	11.4
	8 ♀	164	68	22.0	26.2	20.0	13.6	4.1	11.1	4.0	5.6	7.3	9.3	3.9	11.2
Lasqueti Island	4 ♂	160	73	21.8	26.0	19.3	13.2	4.0	10.8	4.0	5.4	7.0	8.8	3.7	11.0
	4 ♀	169	78	22.0	27.2	20.3	13.6	3.9	11.3	4.1	5.6	7.3	9.5	3.9	11.5
Thormanby Island ...	4 ♂	170	83	22.4	25.7	19.5	13.2	4.2	10.6	3.9	5.7	7.1	9.1	3.7	11.2
Bowen Island	10 ♂	174	78	21.6	26.3	20.3	13.6	3.9	10.6	4.0	5.5	7.4	9.4	4.0	11.1
	4 ♀	172	77	21.6	26.1	20.2	13.4	4.1	10.6	3.9	5.6	7.5	9.4	3.9	10.9
Saturna Island	6 ♂	175	69	20.5	26.5	19.9	13.5	4.0	11.1	3.8	5.5	7.1	9.4	4.0	10.6
	4 ♀	161	62	20.5	24.9	18.7	13.1	3.9	10.5	3.7	5.3	6.8	8.6	3.9	10.6
Vancouver Island ...	5 ♂	175	89	21.0	25.0	19.0	12.8	3.8	10.3	3.6	5.2	6.9	9.0	3.6	10.7
	5 ♀	178	88	20.6	25.2	19.3	12.8	3.9	10.6	3.9	5.3	7.0	8.9	3.7	10.7
Mainland (Vancouver)	5 ♂	178	93	21.4	26.1	19.9	13.4	4.0	10.8	3.9	5.5	7.3	9.4	3.7	10.9
	5 ♀	177	94	21.2	26.1	20.1	13.3	4.0	10.6	3.8	5.6	7.3	9.4	3.8	10.8

The differences mentioned are more exactly shown in the table of measurements. Differences due to age, sex and season have largely been excluded.

Specimens examined. Total number, 81, as follows: Vanada, Texada Island, 11; Anderson's Cove, Texada Island, 15; Savary Island, 19; Lasqueti Island, 8; Thormanby Island, 4; Bowen Island, 24.

Variation between Insular Populations of *Peromyscus*

Savary Island population. Skull long and narrow as in topotypical *georgiensis,* with the greater mastoidal breadth of that race; zygomatic breadth averages less than in *georgiensis* and, relative to greatest length of skull, less than in any population studied; body length intermediate but nearer *austerus* of mainland; length of tail almost exactly intermediate.

Thormanby Island population. Skull shorter (over all, as well as in diastema and postpalatal length) and narrower across zygomata than in either *georgiensis* or *austerus;* agrees with *austerus* in shorter nasals but with *georgiensis* in longer palatal slits and greater mastoidal breadth; interorbital breadth averages more than in any other population studied; body only slightly longer than in *austerus* and much shorter than in *georgiensis;* tail of intermediate length, but nearer *austerus.*

Bowen Island population. Skull essentially as in *austerus* of mainland except for longer maxillary tooth rows and slightly greater average length over all, shelf of bony palate intermediate between *austerus* and *georgiensis,* and diastema longer than in either; body almost as long as in *georgiensis;* tail intermediate, but much nearer *georgiensis.*

Lasqueti Island population. Skull essentially as in *georgiensis* rather than as in *angustus* of nearby Vancouver Island; body short, only a little longer than in *angustus;* tail of intermediate length, but nearer *georgiensis.* The animals from Lasqueti Island are compared with *angustus* of Vancouver Island rather than with *austerus* of the mainland because of the nearness of Lasqueti

Island to Vancouver Island. Actually, in certain respects the animals from Lasqueti Island are more like *austerus* than *angustus*. The data presented in Table 1 permit of comparing these two as well as any other two kinds here discussed.

Geographically (see Fig. 1), the insular populations of mice in Georgia Strait have the race *austerus* as a neighboring relative on the mainland to the eastward, and the race *angustus* on the large land mass of Vancouver Island to the westward (*interdictus* appears to be restricted to the higher parts of Vancouver Island). From these two races, the 6 insular populations discussed all differ in longer body, shorter tail and larger skull. Even *angustus* of Vancouver Island, an island of large area with its northern end only narrowly separated from the mainland, averages longer of body and shorter of tail than the mainland *austerus*. Of the 6 insular populations, *P. m. saturatus* from Saturna Island appears to be the most strongly differentiated and in a sense is also geographically segregated, for it is far south of the other small islands mentioned.

The islands are thought to be relatively young geologically and to have been formed by the subsidence of the land, so that now only the higher parts remain as islands. Possibly, then, the parents of the mice on any one island, or on all the islands, were part of a mainland stock eventually isolated by the introduction of a water barrier. Proof of this is lacking, however, and it may be that ancestors of the mice were "rafted" to the already formed islands. Conceivably, their presence is to be accounted for by both means.

It is supposed, at this writing, that the morphological features differentiating these 6 insular populations of *Peromyscus* result from fortuitous genetic variations persisting under isolation. It is thought that without isolation several of the existing variations never would have become established; the variations probably would have been swamped as a result of cross-breeding with mice

from adjoining areas. To me, there is strong evidence that isolation has played a part in the differentiation of these mice, and I can imagine some details of its operation. The exact ways in which natural selection may have operated to establish the differences found beween populations, are less easily imagined in the absence of ecological facts for correlation with the morphological information furnished by study of the specimens. Indeed, the failure of natural selection to act at all on certain mutations may account for some of these variations which have persisted.

In this instance, even if the naturalist were able to perceive all the things that are "selected for by nature," possibly he could not explain why the farther the island

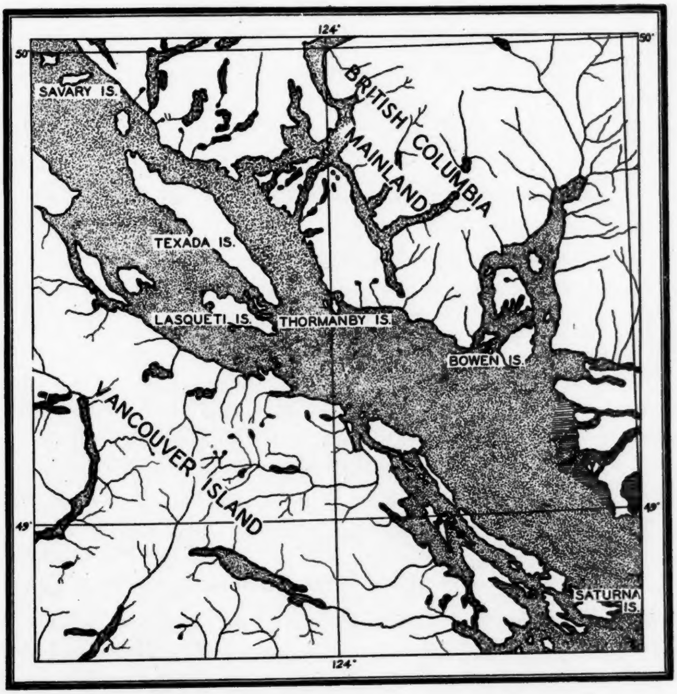

Fig. 1. Map of the Georgia Strait region of southwestern British Columbia, showing islands from which small mammals mentioned in the text are available.

is from the mainland, the longer is the mouse's body and the shorter its tail. The correlation in this respect is such that, given the distance of the island from the mainland, he might closely predict (save for Lasqueti Island; see next paragraph) the lengths of bodies and tails of mice on islands from which specimens, as yet, are not available. The islands from which mice are available, arranged in order of increasing distance from the mainland, together with head-body-length and tail-length, are as given in Table 2.

TABLE 2

	Mainland (Vancouver)	Thormanby Is.	Savary Is.	Bowen Is.	Texada Is.	Lasqueti Is.	Saturna Is.
Distance (miles) .	0	$\frac{3}{4}$	1	2-$\frac{1}{2}$	2-$\frac{3}{4}$	11	14
Body-length	84	87	89	96	98	89	103
Tail-length	94	83	82	78	69	76	66
$\frac{\text{Tail}}{\text{Body}}$	112%	95%	92%	81%	70%	85%	64%

The one exception, of a sort, is Lasqueti Island, 11 miles off shore. If Vancouver Island had no *Peromyscus,* Lasqueti Island, only 6$\frac{1}{4}$ miles away, might then entirely conform to the rule, for, possibly, its *Peromyscus* are "contaminated" by the short-bodied, long-tailed, mice from Vancouver Island, which to the northward is only narrowly separated from the mainland, and which is a land mass of so great a size as to be in a category apart from that of the other, smaller islands. Even so, Lasqueti is far enough off-shore from Vancouver Island that, on the basis of known trends in these insular mice, one would expect the head-body length to be greater and the tail length to be less than it is, even though *some* modification is actually shown in the direction expected.

MEADOW MICE (*Microtus*)

Microtus townsendii cummingi Hall (1936): A series of 11 specimens, including 9 adults, from Texada Island, are referred to this race. These mice agree with topotypical *cummingi* in relatively broad mastoidal region, shape and size of nasals, construction posteriorly of incisive foram-

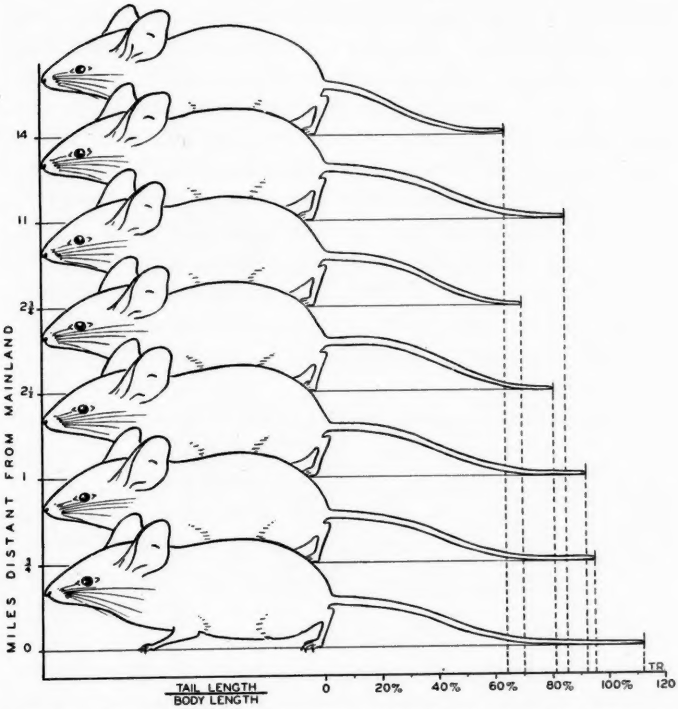

FIG. 2. Diagram showing decreasing tail length with increasing distance from mainland of populations of *Peromyscus maniculatus,* in Georgia Strait. See Table 2.

ina, broad rostrum and large size. The size averages even greater than in topotypical *cummingi,* and the dorsal outline of the skull, in longitudinal axis, is still more convex. These two variations are more extreme developments of features that distinguish topotypical *cummingi* of Bowen Island from its near relatives, *townsendii* of the mainland and *tetramerus* of Vancouver Island.

In the animals from Texada Island the length of the tail averages about the same as in *cummingi,* but relative to the body length it is shorter. This feature, and the longer, as well as broader, exposed portions of the upper incisor teeth, are the only features found which might be

regarded as unique; the other characters noted are present in one or another of the three populations, from Vancouver Island, Bowen Island or the mainland. Possibly each of these is the result of differential growth (for full exposition of this principle see Huxley, 1932); that is to say, features to be expected in an individual from Bowen Island should it attain the greater over-all size of one from Texada Island. In review: the *Microtus* from Texada Island in general have developed more pronouncedly than have animals from Bowen Island, the characters mentioned in the original description of *cummingi* as differentiating it from its two relatives, *M. t. townsendii* and *M. t. tetramerus.*

Average and extreme measurements of adults from Texada Island, 4 males and 5 females, are as follows: Total length, male 192(185–203), female 186(179–193); length of tail, 56(54–59), 53(42–58); length of hind foot, 25.0(24.0–26.0), 23.5(22.5–25.0); basal length including incisors, 29.7(28.7–29.4), 29.2(29.0–29.9); zygomatic breadth, 17.9(17.4–18.4), 17.7(17.0–18.1); mastoidal breadth, 13.7(13.4–14.0), 13.3(12.9–13.7); length of nasals, 8.9 (8.8–9.1), 8.6(8.2–8.9); greatest width of rostrum, 6.0(5.8–6.1), 5.9(5.7–6.1); alveolar length of upper cheek teeth, 7.9(7.7–8.1), 7.8(7.6–8.0).

Shrews (*Sorex*)

Five shrews are available from Texada Island. These are of the species *Sorex obscurus,* which ranges widely over the mainland to the eastward and occurs also on Vancouver Island. The sample from Texada Island, however, reveals that the animals there have shorter tails than those on the mainland and are characterized by other structural features that warrant the recognition of a distinct insular race. This may be known as:

Sorex obscurus mixtus new subspecies

Type. Male, adult (moderately worn teeth), skin and skull; no. 70376, Mus. Vert. Zool.; Vanada, Texada Island, Georgia Strait, British Columbia; May 4, 1936; collected by R. A. Cumming; original no. 1501.

Range. Known only from the type locality.

Diagnosis. Size medium; color dark; hind foot short (13 mm. or less); palate long (7 mm. or more).

Comparisons. Color much as in *Sorex obscurus isolatus* of Vancouver Island and *Sorex obscurus setosus* of the adjoining mainland; hind foot smaller and palate

longer than in either; tail about as in *isolatus* and shorter than in *setosus;* length over-all about as in *Sorex obscurus obscurus.* Compared with *Sorex obscurus longicauda, mixtus* is smaller, although the length of the palate approaches that of smaller specimens of *longicauda.*

Measurements. Five specimens, one lacking the skull, from Vanada, present average and extreme measurements as follows: Total length, 111 (108–117); tail vertebrae, 48(44–49); hind foot, 12(12–13); condylobasal length, 17.3(17.1–17.6); palatal length, 7.1(7.0–7.2); cranial breadth, 8.5 (8.4–8.7); least interorbital breadth, 3.3(3.2–3.4); maxillary breadth, 5.0 (4.8–5.2); maxillary tooth-row, 6.3(6.2–6.3).

Remarks. The abundant material in the Museum of Vertebrate Zoology from Vancouver Island and Mr. Cumming's fortunate acquisition of a series from the mainland approximately opposite Texada Island have made the comparison of this insular material relatively simple. The shorter tail of *mixtus* parallels the shortening of the tail in *Peromyscus* from the same place. Yet, unlike the condition found in *Peromyscus,* the length of body and length of skull appears to be no more than in the mainland population.

Specimens examined. Five from the type locality.

Sorex vagrans vancouverensis Merriam. Ten specimens are available from Bowen Island. In the average of their coloration they are nearer to *S. v. vancouverensis* than to *S. v. vagrans* of the mainland. Other than in color, no differences have been found to separate these animals from the stock on the mainland.

LITERATURE CITED

Engels, W. L.
1936. *Am. Midland Nat.,* 17: 776–780, July, 1936.

Hall, E. R.
1936. *The Murrelet,* 17: 15–16, for January. March 28, 1936.

Huxley, J. S.
1932. "Problems of Relative Growth." The Dial Press, New York. Pp. i–xix + 1–276, 105 figs. in text. 1932.

Snedecor, G. W.
1934. "Calculation and Interpretation of Analysis of Variance and Covariance." Colgate Press Inc., Ames, Iowa. Pp. 1–96. 1934.

Turnbull, J. D.
1937. [In memoriam—R. A. Cumming] *The Murrelet,* 18: 33.

SOME ASPECTS OF THE BEHAVIOR OF THE FRESH-WATER JELLYFISH, CRASPEDACUSTA SP.[1]

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THE discovery of large numbers of fresh-water medusae in an artificial lake near Lynchburg, Va., rendered possible the observation of living jellyfish in the laboratory, a somewhat unusual event. That these jellyfish belong to the genus Craspedacusta of Lankester seems reasonable, but since many specimens measured were as much as 90 per cent. larger than the largest Craspedacusta described, their inclusion in any known species would at present require a stretch of the imagination.

The medusae were discovered in the lake in large numbers about August 5, 1937, and were observed there at frequent intervals until October 7, 1937, when no more were visible. As many as seventy fair to large sized specimens have been counted in each cubic meter of surface water. On other days, few medusae were seen except in the wake of the boat or where the water had been stirred to some depth by means of a paddle.

Crystal Lake itself is approximately square (Fig. 1) and varies considerably in depth. It filled in above an earthen dam which restrains a very small stream and has been in existence some ten years. The pond was stocked with fingerling bream and black bass two years ago, and a dense plant growth followed. Although the vegetation was largely cleared out last year, the bottom where shallower than two meters is densely covered with Utricularia, and this plant is found even in the deepest parts. The water has a high organic content, a green Stentor and a Spirostomum being very conspicuous protozoans occurring there in great numbers. Parts of the lake where the depth

[1] A paper read before the thirty-fifth annual meeting of the American Society of Zoologists (General Physiology Section) at Indianapolis, Ind., December 28, 1937. (Introduced by J. I. Hamaker.)

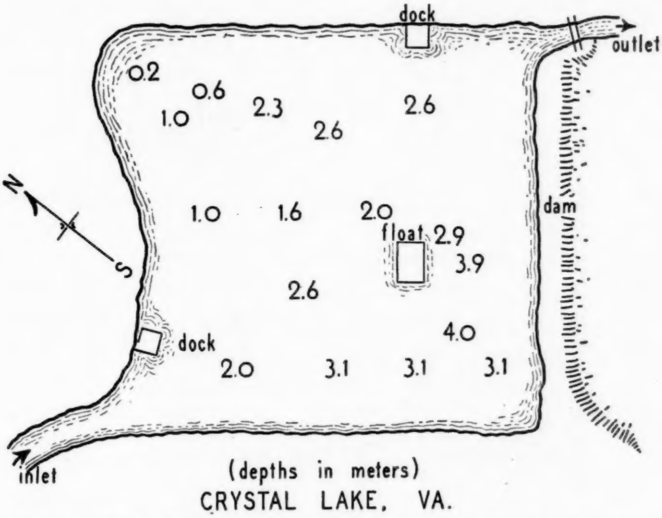

FIG. 1. Crystal Lake is 14 miles southwest of Lynchburg, and measures approximately 150 feet each way. The jellyfish were most numerous around the diving float.

is greater than two meters were well populated with medusae; between one and two meters they were less common, and in less than a meter of water they were always rare. A search for hydroids was unsuccessful. All medusae appear to be females, and measured as much as twenty-two millimeters in diameter. The water temperature prior to the disappearance of the medusae was as much as 25° C., but dropped to 14° C. after a short cold period prior to October 7.

The gross movements of the medusae are chiefly vertical ones, due to the shape of the animal rather than to selective swimming. Lateral movements in the water allow the jellyfish to sideslip so excessively that progression in a horizontal line is turned by gravity into a sharp descent. When the diameter of the bell is horizontal, the jellyfish may be swimming either up or down. If upwards, the reaction with gravity results in the motion illustrated by Fig. 3, the umbrella-like form helping the

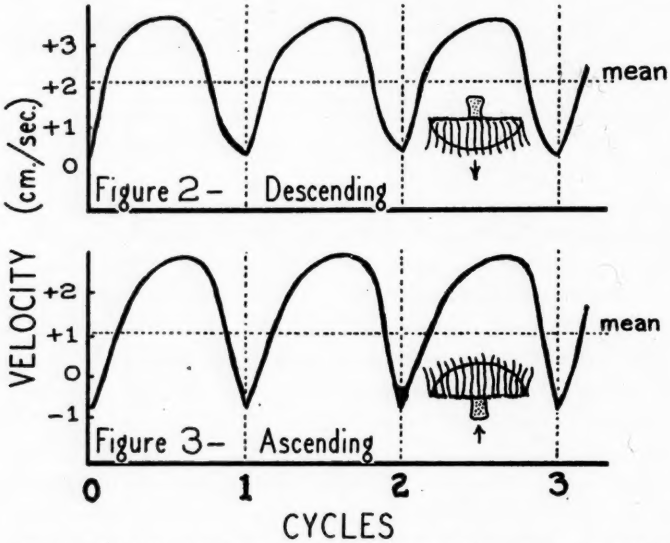

FIG. 2. Variations in velocity of medusae making a "power dive" during the phases of the contraction cycle.

FIG. 3. Variations in velocity of medusae ascending at full speed, in the phases of the contraction cycle.

animal not to lose during a recovery phase the distance gained during the preceding contraction. If the medusa be swimming downward, the net speed is nearly doubled, but the water resistance now slows the motion of the animal between contractions of the bell, so that the speed varies as in Fig. 2. The average number of contractions per second in any direction is about one, and the average upward speed at this rate approximates thirty-six meters per hour.

After twenty to twenty-five successive contractions, the jerking movements become much less violent and the rate is noticeably reduced as fatigue apparently sets in. Resting medusae frequently settle through the water in a horizontal position, in which case their speed is about one third of that in upward progression. In sideslipping, however, the rate is in excess of that during a "power dive." When settling mouth downward, the bell often flattens out, so

that the manubrium extends farther below the rim than under any other circumstances. At such times, too, the velum hangs vertically downward.

Jellyfish falling to the bottom of the aquarium may strike against the side or touch the outstretched branch of a plant, this giving enough turning moment to rotate the animal through as much as 180°. No reaction to such gentle contact has been noted, which may indicate that the so-called lithocysts do not stimulate the medusa in any profound manner. Furthermore, medusae which reach the bottom with the manubrium upward may pulsate for some time before an asymmetric contraction rotates them into a position from which they can progress. In such asymmetric contractions, it is the velum rather than the bell itself which is responsible for the changed direction of the expelled water. That such movements while bumping against the bottom are respiratory rather than locomotory is not a very plausible explanation, since medusae restricted from further downward movement by plant fibers frequently continue their efforts until the fibers separate, allowing passage for the animal.

The reaction to light seems no more pronounced than that to gravity. Both in the aquarium and in the lake, there was no observed migration of the animals which could be correlated with sunlight, skylight, shade or artificial illumination. The general activity of the jellyfish during the night seems no different from that noted during the day. That sunlight did not affect the animals suggests that they are not very responsive to moderate changes in temperature, since the water in the lake warms up considerably during a clear day. It was noted that a surface temperature of 25° C. was tolerated in the lake, but that all specimens in an aquarium died and promptly shriveled when the water temperature approached 30° C. Specimens placed in the refrigerator at a temperature of 9° C. showed feeble contractions when stimulated by water currents, but fully recovered their locomotor pulsations after an experience of several hours duration, as soon as

the temperature reached 17° C. Obliteration of normal contractions took place at about 15° C. when cooling contracting medusae in the refrigerator.

Superficially the several sets of tentacles appear to be of two types, long ones from a half to three quarters as long as the diameter of the bell, and short ones less than one fifteenth of the bell's diameter. The longer types make a crown for the medusa, held either vertically or slanting to 70° from the horizontal. The shorter types are either pendulous or held horizontally as a lateral fringe. The position of the longer tentacles seems to be characteristic of even small specimens of this species. No use of the tentacles in feeding was observed, although they are well supplied with nematocysts. No irritation was noted following contact of tentacles upon human skin.

The four gonads, one on each radial canal, are roughly triangular bags, somewhat similar to pistol holsters. Maintaining this simile, the barrel of the pistol would fit in the lateral portion of the gonad, the butt pointing toward the middle of the bell, the muzzle pointing ventrad (if the manubrium does also). The opening at the top of the gonad pouch is very apparent and seems to be supplied with stiffening structures which hold it open to the gastrovascular cavity. The gonads are pendant and fold easily upon themselves when in contact with any firm object. The genital epithelium is entirely superficial. In specimens exposed to temperatures below 12° C. the reproductive tissue died, swelled and was shed without appearing to inconvenience the animals.

The manubrium apex is somewhat four lobed, but each of these is thrown into a larger number of folds which may assist the animal in feeding. When the medusa contracts and is thereby moved through the water with some speed, the tip of the manubrium lags behind as the body of this structure elongates. When the contraction phase is over and the medusa is preparing for the next jerk, the manubrium tip rapidly approaches the bell and its body becomes much stouter and shorter. This change in shape

may best be thought to correspond to the motion of water from the cavity of the bell. When the contracting bell forces the water away from the jellyfish in a stream, the manubrium is drawn with the current, but as soon as the current ceases, the manubrium regains its shape, displaying a certain amount of elasticity, no doubt aided by the gradual replacement of water within the cavity of the bell. No independent movement of the manubrium was noted, although it was looked for on many occasions. At odd times, miscellaneous trash from the bottom of the aquarium was seen adhering to the manubrium of specimens, but no indication of a feeding movement could be seen to follow these adhesions.

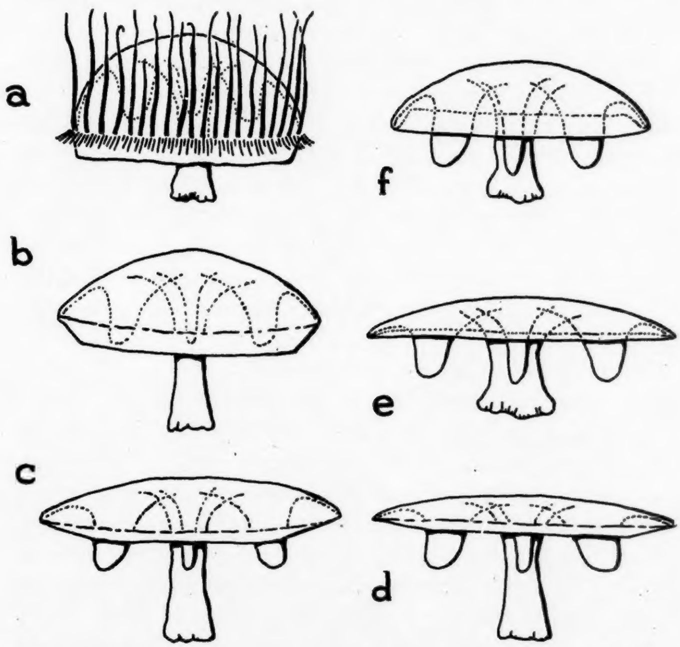

FIG. 4. Phases in the contraction of the medusae, with special attention to the shape of the bell, the position of the velum and the proportions of the manubrium. The tentacles have been omitted from all but Fig. *a*. Figs. *a*, *b*, *c*, *d*, contraction phase, Figs. *e* and *f* recovery phase.

The motion of the velum during the contraction cycle was a much more active and coordinated movement than would be expected from study of preserved medusae or than can be seen from watching velate medusae in the sea. At the beginning of contraction, the velum hangs almost vertically downward and the bell is of maximum height and hence volume. As the bell decreases in height, forcing the water out parallel to the pendant manubrium, the velum also contracts, so that the diameter of the bell is reduced. This contraction of the velum, however, seems principally on its inner margin, causing it to take the form of a band slanting downward and inward at about 45° to the horizontal all around, thus effectively controlling the direction of the outgoing water. This obtains for the jellyfish the greatest effect of the current by restricting it into a jet. As the contraction is completed, the velum comes to have the position seen in preserved material, being horizontal, extending toward the manubrium from all sides. Presumably this is the stage of maximum contraction. In the recovery phase, as water is once more drawn into the bell, muscular control of the velum is apparently omitted, since it is carried into the cavity of the hemisphere, and does not settle into its pendulous condition until the bell is once more full and ready for the next contraction.

It would be interesting to know just how these jellyfish feed. Foods must enter the opening at the tip of the manubrium, between the folds of the lobes. Yet the locomotory movements of the animal must cause much potential food to rush past the opening. Much of the time spent on the bottom would seem to be of no use in feeding, since the manubrium is stretched upward and not in contact with the detritus on the substratum. Perhaps the chief feeding time is when the medusa is drifting downwards with the bell greatly flattened, the velum, gonads and manubrium pendant. Without some active movement on the part of the manubrium, however, it is doubtful if much of the microscopic food would enter; most would

surely follow the water currents around the sides of the slowly advancing structure. It would seem odd also that this type of drifting is not the commonest movement of the animal, if it were of such significance in food-getting. For this reason, and little else, I am of the opinion that the jellyfish obtains its food from the eddy which is set up at the end of the blunt manubrium when the water current from the contracting bell is passing it. This type of feeding could go on at each contraction irrespective of the position of the individual. It would also correspond to what is probably a respiratory current and suggest a method which would not be dependent upon nearness to larger vegetation or the bottom of the pond or stream, but solely on the frequency of food particles in the water. Adhesion of food to mucus on the manubrium is probable, followed by movement of the loaded films into the gastrovascular cavity.

Miss Libbie Hyman, of the American Museum of Natural History, has called my attention to my misuse of the word gonosome in referring to the gonad-bearing stage or medusa. "The word gonosome is not synonymous with medusa. . . . The gonosome of a hydroid species is a collective term for all those parts of the species concerned with sexual reproduction, namely, the medusa-buds, blastostyles, gonangia and gonophores of all description. . . . The gonosome of Craspedacusta would therefore mean the medusa-buds plus the medusae." I am pleased to take this opportunity of correcting my error in the paper cited below. The misuse was not original, but occurs in other articles listed.

LITERATURE CITED

Aitken, W. W.
1936. *Science,* 83: 187.

Baird, R. L.
1932. *Ohio Jour. Sci.,* 32: 323–324.

Brooks, S. T.
1932. *Science,* 76: 465.

Browne, E. T.
1906. *Quart. Jour. Mic. Sci.,* (n.s.) 50: 635–645, pl. 37.

Garman, H.
1916. *Science,* 44: 858–860.
1924. *Science,* 60: 477–478.
Hamaker, J. I., and L. J. Milne
1937. *Science,* 86: 494.
Hargitt, C. W.
1907. *Science,* 26: 638.
Kraatz, W. C.
1933. *Science,* 77: 87.
Kuster, K. C.
1938. *Science,* 87: 300.
Mayer, A. G.
1910. ''Medusae of the World,'' Vol. 2, p. 363.
Ortenburger, A. I., and G. R. Phillips
1931. *Science,* 74: 222.
Payne, F.
1924. *Jour. Morph.,* 38: 387–430, 10 pls., 74 figs.
1926. *Biol. Bull.,* 50: 433–443.
Pratt, H. S.
1935. ''Manual of the Common Invertebrate Animals,'' p. 132.
Quick, B. E., and D. C. Matthews
1937. *Science,* 86: 561.
Robertson, I. C.
1934. *Science,* 80: 403.
Smith, F.
1925. *Science,* 61: 588–589.
Stoner, D.
1938. *Science,* 87: 188.
Viosca, P., and M. D. Burkenroad
1936. *Science,* 84: 155–156.
White, W. E.
1930. *Biol. Bull.,* 59: 222–232.
Woodhead, A. E.
1933. *Science,* 78: 479.

SHORTER ARTICLES AND DISCUSSION

THE NATURE OF CERTAIN SUPPOSED SEX CHROMOSOMES

THESE structures, characterized by either differences in number (XO) or structure (XY), were first clearly distinguished by Wilson in 1905 and 1906. In the first type (the only one considered in the present communication) in the reduction division of the first meiotic mitosis one or more of the chromosomes lag behind the rest and pass exclusively to one of the daughter cells. As a result of this unequal division the other daughter cell has one or several, as the case may be, fewer chromosomes than its sister cell. It is generally supposed that as the second spermatic division sets in, the inequality resulting from the first division is exactly maintained, so that the resulting sperms are two containing the identical excess number of chromosomes and two carrying the deficient chromosomal equipment. The twins of the former type are considered to be female-producing sperms and the latter male-producing sperms.

The genus Ascaris has for many years been taken as an exemplar of general chromosomal relations, both in the case of the somatic and reproductive cells. A marked instance of this tendency is exemplified in the title of a recent general zoological work entitled "Ascaris," the author of which, an international biologist, is now domiciled in the University of California.

It is the purpose of the present note to make clear that the course of events in Ascaris has in a number of instances been quite erroneously described by those cytologists who have dealt with its spermatogenesis. To avoid the errors of wishful thinking photographic illustrations are supplied of the first and second meiotic divisions of the sperm mother cells of *A. lumbricoides*, as found in the pig, man, etc. Fig. I illustrates at high magnification the first meiotic division. The anaphase or early telophase is shown. It is clear from the inspection of the highly magnified photomicrograph that together with chromatic material which has been distributed into the daughter cells in various stages of development, other chromatin is found either on the line of separation of the two daughter spermatocytes, or enclosed in one or the other of these. The latter stage may be observed either on the upper left or the lower right of the figure.

This is in accordance with the received view of the course of spermatogenesis in the species under discussion. The lagging chromatic material can be seen under higher magnification than that shown in the photomicrograph to consist of five chromosomes so that the secondary spermatocytes in this species contain 19 and 24 chromosomes, respectively. With this conclusion we are in agreement.

The description of the second reductional or reproductive divisions in the spermatogenesis of the species under consideration, however, have been described entirely erroneously. Here again

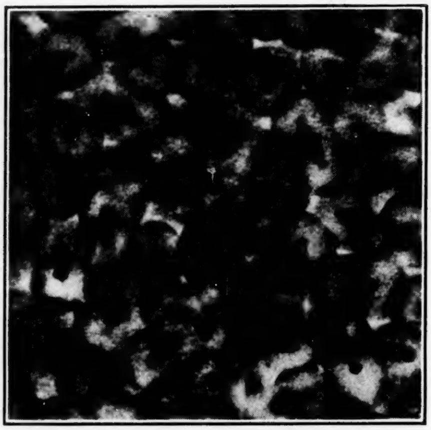

FIG. 1.

a photomicrograph supplies objective evidence in regard to the real course of events. The magnification is the same as in the first figure, and it is clear that the cells involved are approximately about one third smaller in diameter than in the first. Inspection of the right-hand side of the figures reveals lagging masses of chromatin already included in one of the daughter cells. In other parts different stages of lagging may be observed. Since the chromatic lagging mass consists here as in the first illustration of a number of chromosomes, the resulting sperms may contain as many as four different equipments of chromosomes, the numbers running from 14 to 21 in cases examined in the present connection. If chromosomal equipment be regarded as the determiner of sex, there ought to be in some instances as many as four or even more sexes in *Ascaris lumbricoides*. The absurdity of

such a conclusion is self-evident. In order to avoid any fallacies based on the study of inadequate material, a huge number of males of the species under discussion have been examined as to their chromosomal behavior. The results in all instances were in harmony with the course of events outlined previously.

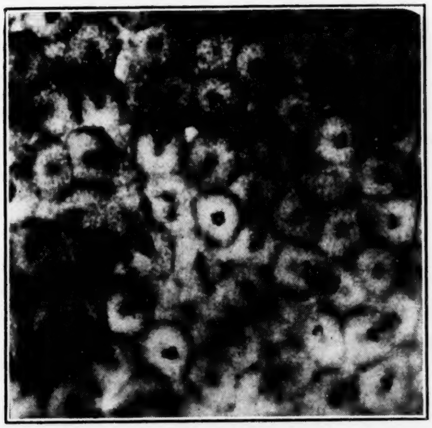

FIG. 2.

As a further check upon the conclusions reached in the case of *A. lumbricoides*, another classic species has been examined, namely, *A. canis*. Here the lagging group in the first reproductive spermatic division is six and the secondary spermatocytes have as a consequence 18 (supposed female-producing) and 12 (supposed male-producing). Just as in the case of the first species here considered the secondary spermatocytic divisions repeated the abnormality of the first and as a consequence instead of the possibility of only two types of sperms, namely, male- and female-producing, there exists a potential realization of more than two spermal chromosomal equipments. As a result the same fallacy as to the determination of sex presents itself.

If the explanation of the abnormal reductional divisions in Ascaris is not the determination of sex, another more probable hypothesis must apparently be sought. It has been known for over thirty years dating from the epochal investigations of Rosenberg, that lagging meiotic chromosomes are often the sequel to interspecific hybridization. Since hybrids of Ascaris are known to exist, hybridization is a reasonable explanation of the abnormal

reduction divisions found in many species of this genus. In the case of interspecific plant hybrids, the lagging is often confined to the first meiotic division. We have found a counterpart to this situation in a species of Ascaris obtained in large numbers by Mr. D. Linehan in a gray seal shot off Marblehead, Massachusetts, and communicated to the authors of the present note. In this species laggards are present only in the first division, as is often the case with interspecific hybrids in plants.

Apparently the most glaring fallacy connected with the so-called sex chromosomes is the attribution to them of the causation of parthenogenesis by Baehr and T. H. Morgan. In *Aphis saliceti,* in which the surviving sperms have only three chromosomes and *Phylloxera caryaecaulis,* with a similar equipment, the secondary spermatocytes with the small (two) numbers of chromosomes abort. Since these authors believe that the only surviving secondary sperm mother cells are the female-producing ones, they consider that the parthenogenetic females, which constitute a large portion of the life cycle of the species, are the result of the abortion of male-producing secondary spermatocytes. This conclusion appears fallacious for two reasons. In the first place, it supplies no explanation of the diploid eggs which are quite generally present in parthenogenesis. Secondly, there are numerous aphids in which there are lagging chromosomes, interpreted by the authors cited above as sex chromosomes, in which there is lagging in both the first and second spermatocytic divisions precisely as in Ascaris described in earlier paragraphs. Furthermore, one of the secondary spermatocytes does not abort. Often all four sperms have the same chromosomal equipment. This situation has been observed by one of us in the case of *Aphis populifoliae* and *Aphis salicicola.* Here parthenogenesis has obviously no relation either to supposed sex chromosomes or abortive secondary spermatocytes.

It may appropriately be added that any adequate chromosomal explanation of parthenogenesis should apply equally well to plants as to animals. There are very numerous cases of parthenogenesis among plants for which this explanation can not possibly be adopted, since there are no sex chromosomes present at all.

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FURTHER INVESTIGATIONS ON THE STRUCTURE OF CHROMOSOMES

In recent years the coiled nature of the structural elements present in chromosomata has been more and more widely recognized as the result of improvement both in methods of fixation and of staining. Of those who have dealt authoritatively with this subject only Darlington in the second edition of his well-known volume, purporting to chronicle recent advances in cytology, adheres to the now apparently obsolete view that the chromosome consists of a ground substance in which are situated serially, in moniliform or necklace-like rows, rounded bodies known as chromomeres (interpreted by several authors as the morphological representatives of the genes). Among more recent investigators as well as some earlier ones, the internal organization of the chromosome has been regarded as essentially spiral. The spirals, of which two are apparently always recognizable where the chromosomes are large enough to permit favorable study according to the more numerous investigators such as Sax, Matsuura, Huskins and Nebel, run parallel to one another. The present authors as the result of a wide study covering both plants and animals and reproductive as well as somatic chromosomes have reached the conclusion that the two spirals present run in opposite directions, precisely as is true when two pieces of rope or rubber tubing are twisted about one another. It would seem at first sight that it should be extremely easy to decide which of these views is correct.

In Fig. 1 is shown a pair of strands of braided rope twisted about one another in opposite directions. In A the strands are loosely coiled and it is quite clear that the strands run in opposite direction precisely as is the case with two cogged pinions. Obviously, if one of the pinions is turned towards the right, its sister pinion will move in the opposite direction, that is towards the left. This situation is practically universally presented by the two coiled chromatids of the longer and more slender and more loosely coiled somatic chromosomes. An extended study of somatic chromosomes in both plants and animals has convinced the present authors that this is a very general if not universal situation. In Fig. 1 B is shown the appearance when the two strands of rope are tightly wound about one another. Here due to the tense winding only the upper turns of the coils are

clearly seen. It accordingly appears that the coils all run in the same direction. This is the situation often presented by the thicker and more voluminous reproductive chromosomes in which the coiling, due to greater thickness and mass of the elements involved, is more tense. Since by far the greatest number of observations on the organization of chromosomes has been made on reproductive cells, by reason of their greater size and easier fixation, it is not surprising that the conclusion has been reached

that the coils or gyres of the chromosomal chromatids run parallel to one another. This conclusion is further strengthened when the smear method of staining and fixation is employed.

As has been indicated above, the somatic chromosomes of plants and animals, by reason of their greater slenderness and looser gyres, present a truer view of the real relations of the two chromatids in general characteristic of all chromosomes. Fig. 2 A shows the advanced anaphase of the somatic mitosis in *Trillium grandiflorum*. On account of the high magnification (about 2,000) only a few of the chromosomes are in sharp focus. The most favorable of these is found on the left side of the upper group of chromosomes constituting the anaphase figure. Here

the crossing of the gyres in opposite directions can without much difficulty be made out. Less clear indications are presented by other chromosomes, less clearly focused. On the right of 2 B can be clearly seen another anaphase in which the magnification is somewhat over 4,000. Here the greater magnification makes clear the mutual relations of the gyres. It is obvious that these cross in opposite directions and thus present a striking re-

semblance to the gyres of the more loosely coiled ropes shown in Fig. 1 A. This is a general situation in somatic chromosomes, as we have ascertained by examination of the sporophytic chromosomes of several species of Trillium (including *Trillium erectum*) as well as those of Tradescantia, Lilium and *Vicia faba,* and also of a number of Gymnosperms, including Pinus, Ginkgo and Cycas. These observations will be detailed elsewhere with appropriate objective photomicrographs as well as interpretive line illustrations.

It will serve as a useful purpose even in the present necessarily brief note to call attention to the bearing of the observations summarized here on general cytogenetic theory. It is now obvious that the so-called chromomere substantially described by Balbiani over half a century ago is nothing more than an illusion based on improperly preserved and stained chromosomes. Even

if we were to regard the crossing the gyres as having a cytogenetic significance in connection with inheritance, we should be met at once with the difficulty that these crossing points are much more than twice as numerous in the somatic chromosomes as in the reproductive ones. Further in the chromosomes, whether reproductive or somatic, the number of crossing points varies in the course of time and is a function of the contraction or elongation of the chromosomes.

It is further clear that with the emergence of a new point of view in regard to the organization of chromosomes, it becomes extremely difficult to adhere to the pairing (synaptic, syndetic) hypothesis of meiosis. It is now apparently clear that the paired condition is primitive or fundamental for the chromatids of the chromosomes at every stage of their existence. Further, the organization of the so-called synaptic mates as revealed by an accurate study of their internal structure as contrasted with that of their mere silhouettes, reveals that they represent not in any sense a fusion of chromosomes, but rather a division of these. This is the view set down for the most part in the cytological literature of a quarter of a century ago or more. This, for example, is the conception put forward in the first edition of Wilson's classic work on the cell in development and inheritance. In this case, as in many others, first thoughts have turned out to be the best.

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OBSERVATIONS ON HIBERNATING BATS WITH ESPECIAL REFERENCE TO REPRODUCTION AND SPLENIC ADAPTATION

Several hundred big brown bats, *Eptesicus fuscus*, and a few bats of other species, *Myotis keenii septentionalis*, *Myotis lucifugus* and *Pipistrellus subflavus*, have been observed hibernating in caves in southern Minnesota. Field data, together with studies on respiration and body temperature, have been reported previously (Evans, 1934, Swanson and Evans, 1936). In brief, it was found that the respiration of an undisturbed hibernating bat proceeds intermittently, periods of apnea 3 to 8 minutes long alternating with periods of 3 minutes or less of breathing at the rate of 25 to 50 inhalations per minute. As a few bats were seen

flying about on all visits to the caves, it is assumed that they occasionally awaken spontaneously. However, considerable stimulation is necessary thoroughly to awaken a fully torpid bat. Such a bat, if disturbed, shows irritation by opening its mouth, baring its teeth and biting anything placed in the mouth. It can not fly. If knocked from its perch, it falls to the ground and may crawl slowly for a short distance. Thirty to 60 minutes of stimulation are necessary to arouse it sufficiently to fly. After this length of time, the bat breathes at a rate of about 200 respirations a minute and the body temperature has risen from within 2 or 3 degrees of the atmospheric temperature (about 45° F) to over 98° F.

On December 31, 1934, twenty big brown bats were collected. Ten of them were killed by crushing the skull before they were aroused. The other ten were agitated until they were fully awake and able to fly, and were then killed by crushing the skull. All were promptly slit open and placed in a solution of formaldehyde. Necropsy of these bats several months later showed them all to have a large amount of fat in the subcutaneous and retroperitoneal tissues. The gastrointestinal tracts were empty except for a small mass of fine granular material just above or in the upper end of the rectum. From gross and microscopic appearance, this seemed to be chitin or sclerotin, probably from the exoskeleton of insects which had been eaten. In one instance a gall bladder that showed no evidence of pathology was distended with bile. The urinary bladder is some cases was distended, but in others was contracted and contained only a few drops of urine. Where bats get water during hibernation is difficult to say. It is possible that they lap the droplets of condensed water which accumulate on the fur while they hang suspended from the roof of the cave.

In males the seminal vesicles projected upward behind the bladder, and were much larger than the prostate. Microscopic studies of testes revealed seminiferous tubules which appeared shrunken and contained only a sprinkling of spermatozoa. The spermatogonia lining the tubules were large but showed no evidence of activity. No stages intermediate between spermatogonia and mature spermatozoa were found. The epididymis was composed of widely dilated tubules packed with spermatozoa. The spermatic duct, also, was filled with spermatozoa. In contrast, a section of testis from a normal male bat collected in mid-

summer showed the seminiferous tubules to be filled with cells of immature stages, including a few spermatids but no spermatocytes. Tubules of the epididymis were patent but empty except for a small amount of secretion from the lining cells. From these findings it is seen that the early stages of spermatogenesis occur in the testis of the bat during summer. Mature spermatocytes are formed only in late summer or fall and are stored in the epididymis until copulation occurs.

Findings in the female reproductive organs correlated with those in the male organs. The uterus of a normal female caught in midsummer was lined by a single layer of endometrial cells which formed comparatively straight unbranched glands. Sections of the same organ from a hibernating bat showed an endometrium with glands considerably deeper, more irregular and more tortuous than in the preceding animal. Most interesting was a mass of spermatozoa and cellular debris in the uterine corpus. Some spermatozoa had penetrated into the edometrial glands, but none were seen in the Fallopian tubes. Sections of ovaries showed many Graafian follicles of various sizes in midsummer as well as in midwinter. In the latter, however, one follicle was much larger than any of the others, being equal in diameter to one third the diameter of the entire ovary. Obviously this follicle was the site of the ovum destined to be liberated by ovulation. No similar large follicle was present in midsummer.

These observations indicate that the big brown bat, like many other species of bat, has a fall mating period when mature females are inseminated. The spermatozoa reside in the female genital tract until ovulation occurs, probably in late winter or early spring. Hartman (1933) has published a summary of reports on the prolonged survival of spermatozoa in the genital tract of females of several other species of bat.

Hearts, lungs and kidneys of hibernating bats, either dormant or awakened, showed no significant differences microscopically from specimens taken in midsummer. A comparison of spleens from dormant bats with spleens from awakened bats showed that this organ has a very important function in hiberation. In the bats which were killed without being awakened, the spleen was large, dark and congested. Microscopically, the Malpighian corpuscles were seen as widely scattered islands of blue in a red sea of blood. In contrast, the spleen of bats which had been

awakened before they were killed was shrunken and contracted. Microscopic examination showed only a minimal amount of blood. The average volume of five spleens taken from bats which had been awakened was 0.06 cc. A spleen from one of the bats which had been killed with the least possible provocation had a volume of 0.43 cc, seven times the average of awakened animals. The average volume of six spleens from bats killed with as little disturbance as possible was three and one-half times the average volume of spleens from awakened animals, although some of the former had partially contracted in spite of efforts to kill the bats before they awakened. From this it is apparent that during dormancy the spleen of the hibernating bat serves as a reservoir for red blood cells. Any disturbance of the animal results in a reflex contraction of the spleen which pours the red cells back into circulation.

Barcroft and his associates (1925) and others (references in Starling, 1936), working chiefly with cats and dogs, have shown that the spleen normally serves as a reservoir for red blood cells and that the volume of the spleen may be reduced by stimulation of the splanchnic nerves. Hemorrhage, carbon monoxide poisoning or other causes of anoxemia result in contraction of the spleen with an outpouring of erythrocytes from the splenic sinuses into the general circulation. Apparently in the hibernating bat this function of the spleen as a reservoir for red blood cells is most highly developed. It would be interesting to know whether this adaptation of the circulatory function of the spleen is general among hibernating animals.

Sections of two endocrine glands, the adrenal and the thyroid, were studied. Both appeared normal. Follicles of the latter were well filled with colloid, and the follicular epithelium showed no evidence of atrophy, hypertrophy or hyperplasia.

The interested reader will find a comprehensive review of the subject of hibernation in Johnson's paper (1931). Rasmussen (1917, 1918, 1923) has published the results of a thorough study of hibernation of the woodchuck and an excellent discussion of the theories of hibernation (1916).

Summary

(1) Bats occasionally awaken spontaneously during the winter, but a dormant hibernating bat may be aroused sufficiently to fly only after 30 to 60 minutes of agitation.

(2) Microscopic study of the reproductive organs of hibernating bats yielded evidence that the big brown bat, like some other species, copulates in the fall, the spermatozoa remaining inactive in the female genital tract several months during hibernation until ovulation occurs.

(3) The spleen functions as a reservoir for erythrocytes during hibernation and contracts promptly when a dormant animal is disturbed.

(4) Thyroid, adrenal and other organs appear normal to gross and microscopic study.

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LITERATURE CITED

Barcroft, J., H. A. Harris, D. Orahovats and R. Weiss
1925. *Jour. Physiol.*, 60: 443–456.

Evans, Charles A.
1934. *Jour. Mammal.*, 15: 240–241.

Hartman, Carl G.
1933. *Quart. Rev. Biol.*, 8: 185–193.

Johnson, George E.
1931. *Quart. Rev. Biol.*, 6: 439–461.

Rasmussen, Andrew T.
1916. *Am. Jour. Physiol.*, 41: 464–482.
1917. *Am. Jour. Anat.*, 22: 475–515.
1918. *Endocrinology*, 2: 353–404.
1923. *Jour. Morph.*, 38: 147–206.

Starling
1936. "Principles of Human Physiology," edited by C. Lovatt Evans. Lea and Febiger, Philadelphia. 831–833.

Swanson, Gustav, and Charles A. Evans
1936. *Jour. Mammal.*, 17: 39–43.